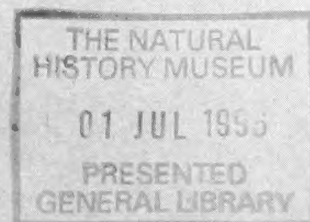


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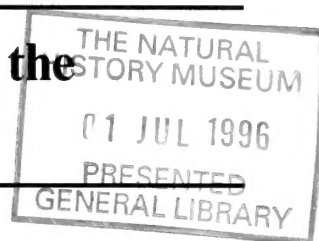
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Deep-sea conoidean gastropods collected by the John Murray Expedition, 1933–34

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SYNOPSIS. Conoidean gastropod molluscs (formerly treated within the family Turridae) from 20 deep-sea (bathyal) stations of the John Murray Expedition (North-Western Indian Ocean) are described. A total of 50 species from 11 families and subfamilies, and 31 genera and subgenera, have been found in the material studied. 17 species are described as new.

ISRN 299727

INTRODUCTION

The John Murray Expedition worked aboard the 'Mabahiss' in the northwestern part of the Indian Ocean in 1933–34 and collected invaluable biological material from the area which has not been subsequently explored on such a large scale. However, no account of the gastropods collected by that expedition have ever been published. Through the courtesy of Dr John D. Taylor of The Natural History Museum, London I was able to study the conoidean gastropods from that collection. This paper deals with deep-sea samples of that part of the Conoidea (= Toxoglossa) which was usually treated as the family Turridae. The Turridae s.l., unlike the Terebridae and *Conus*, are very characteristic of the deep-sea molluscan fauna, of which they comprise a considerable part. The material studied was previously loaned to the late A.W.B. Powell who mentioned some of the species in two parts of his revision of Indo-Pacific Turridae (Powell, 1964, 1969). However, none of Powell's species identifications was found on labels accompanying the samples.

MATERIAL AND METHODS

The molluscs studied were collected at 20 bathyal (depth 183–2312 m) stations of H.E.M.S. 'Mabahiss' in the North-Western Indian Ocean (Table 1). The classification of Conoidea used in the present paper follows that adopted by Taylor *et al.* (1993). All the material including the type specimens of the new species is stored in the Natural History Museum.

ABBREVIATIONS USED IN THE TEXT

| | |
|-----|------------------------------------|
| NHM | The Natural History Museum, London |
| JME | John Murray Expedition |
| H | shell height |
| D | shell diameter |
| Hs | spire height |
| Hb | body whorl height |
| Ha | aperture height |

TAXONOMY

Family **DRILLIIDAE** Morrison, 1966. ICZN pending

Genus **DRILLIA** Gray, 1838

Type species: *Drillia umbilicata* Gray, 1838 (subsequent designation Gray, 1847)

Drillia altispira Sysoev, new species

Figs 18 & 19

MATERIAL. stn 176, 1 shell (holotype, No. 1993088).

DESCRIPTION. The shell is rather large, claviform, with very high spire exceeding half of the shell height, thick and solid, light-brown, consisting of almost 12 whorls. The protoconch is missing. The whorls are weakly convex and slightly angled; the point of angulation is situated below the periphery in the spire whorls, but shifts upwards on the last whorls. The subsutural slope is concave, and the prominence of concavity increases towards the body whorl. Sutures are clear, straight, and shallow. Axial sculpture consists of oblique, narrowly crested folds terminating on the subsutural slope. Some folds form weak nodules just below the suture. The folds become subobsolete on the last quarter of body whorl, probably as a result of preceding shell damage. There are 14 folds on the penultimate whorl and about the same number on the body whorl. Spiral ribs are numerous, uniform, rounded, moderately strong, with interspaces equal to them in width. The ribs cover the entire shell surface but become narrower, closer, and weaker on the subsutural slope. The shell base forms a weak bend in passing to a moderately developed fasciole. The aperture is rather small, inversely pyriform, with a distinct stromboid notch. The outer lip with a thin edge, projects strongly and forms an alate expansion between the anal sinus and stromboid notch. There is no prominent prelabral varix, only a thin fold curved in correspondence to growth lines is present. The inner lip is covered by thick and wide glossy callus which is mostly free along its outer edge and forms a shallow false umbilical cavity. The parietal callus pad is large and rounded, constricting the entrance to the anal sinus. The anal sinus is deep, U-shaped, with spout-like edge, directed slightly adapically. The canal is short, slightly bent to the right, shallowly notched and obliquely truncated. H = 37.9, Hb = 17.5, Ha = 14.2, D = 11.4 mm.

Table 1 Stations of H.E.M.S. 'Mabahiss' where deep-sea conoideans were collected.

| No. | Position | | Area | Date | Depth, m | Gear |
|-----|------------------------------|-------------------------------|--------------|------------|-----------|------|
| 26 | 12°29'30" N, | 50°51'30" E | Gulf of Aden | 11.10.1933 | 2312 | AT |
| 33 | 13°41'00" N, 13°40'00" N, | 48°17'00" E to 48°18'00" E | Gulf of Aden | 15.10.1933 | 1295 | AT |
| 34 | 13°05'36" N, | 46°24'42" E | Gulf of Aden | 16.10.1933 | 1022 | AT |
| 35 | 13°14'24" N, 13°13'24" N, | 46°14'12" E to 46°10'00" E | Gulf of Aden | 16.10.1933 | 457–549 | OT |
| 42 | 17°26'00" N, | 55°49'00" E | Hadramaut | 27.10.1933 | 1415 | TD |
| 62 | 22°53'30" N, 22°56'30" N, | 64°56'10" E to 64°56'30" E | Gulf of Oman | 18.11.1933 | 1893 | AT |
| 106 | 05°38'54" S, 05°40'18" S, | 39°15'42" E to 39°17'36" E | Zanzibar | 12.01.1934 | 183–194 | AT |
| 107 | 05°15'30" S, 05°17'14" S, | 39°33'00" E to 39°32'48" E | Zanzibar | 12.01.1934 | 421–457 | AT |
| 118 | 04°05'54" S, 04°17'00" S, | 41°10'12" E to 41°11'48" E | Zanzibar | 17.01.1934 | 1789 | AT |
| 119 | 06°29'24" S, 06°32'00" S, | 39°49'54" E to 39°53'30" E | Zanzibar | 19.01.1934 | 1207–1463 | AT |
| 122 | 05°21'24" S, 05°22'36" S, | 39°23'00" E to 39°22'18" E | Zanzibar | 22.01.1934 | 732 | OT |
| 143 | 05°15'48" S, 05°13'42" S, | 73°22'48" E to 73°23'36" E | Maldive Is. | 30.03.1934 | 797 | AT |
| 145 | 04°58'42" S, | 73°16'24" E | Maldive Is. | 02.04.1932 | 494 | AT |
| 158 | 04°42'30" S, 04°36'48" S, | 72°42'30" E to 72°48'54" E | Maldive Is. | 07.04.1934 | 786–1170 | AT |
| 176 | 12°04'06" N, | 50°38'36" E | Gulf of Aden | 02.05.1934 | 665–732 | AT |
| 180 | 12°03'24" N, | 50°40'12" E | Gulf of Aden | 02.05.1934 | 397 | G |
| 184 | 14°36'06" N, 14°38'42" N, | 51°00'18" E to 50°57'42" E | Gulf of Aden | 04.05.1934 | 1270 | AT |
| 185 | 13°48'06" N, 13°48'36" N, | 49°16'48" E to 49°16'24" E | Gulf of Aden | 05.05.1934 | 2000 | AT |
| 188 | 13°43'18" N, 13°46'00" N, | 47°56'54" E to 47°50'42" E | Gulf of Aden | 06.05.1934 | 528 | AT |
| 193 | 13°06'12" N, 13°03'00" N, | 46°24'30" E to 46°21'42" E | Gulf of Aden | 07.05.1934 | 1061–1080 | AT |

AT – Agassiz trawl, OT – otter trawl, TD – triangular dredge, G – grab.

The new species resembles *Drillia tasconium* Melvill & Standen, 1901 from the Persian Gulf but differs in the high spire, larger and more solid shell, and absence of spiral sulci which deeply furrow the subsutural area in *D. tasconium*.

DISTRIBUTION. Gulf of Aden, 655–732 m.

Genus *HORAICLAVUS* Oyama in Taki & Oyama, 1954

Type species: *Mangelia splendida* A.Adams, 1867 (original designation)

Horaiclavus splendidus (A.Adams, 1867)

Figs 20 & 21

Mangelia splendida A.Adams, 1867, p. 309, pl. 19, fig. 24.

Horaiclavus splendidus (A.Adams) – Shuto, 1965, p. 154–155, pl. 29, figs 13–15, text-figs 3, 5; Powell, 1966, p. 142, pl. 23, fig. 13; Habe, 1970, p. 120, pl. 38, fig. 13; Kuroda *et al.*, 1971, p. 212–213, pl. 55, fig. 4; Shuto, 1975, p. 166, pl. 6, fig. 17.

TYPE LOCALITY. Goto Islands, Japan.

MATERIAL. stn 176, 3 shells; 188, 1 shell.

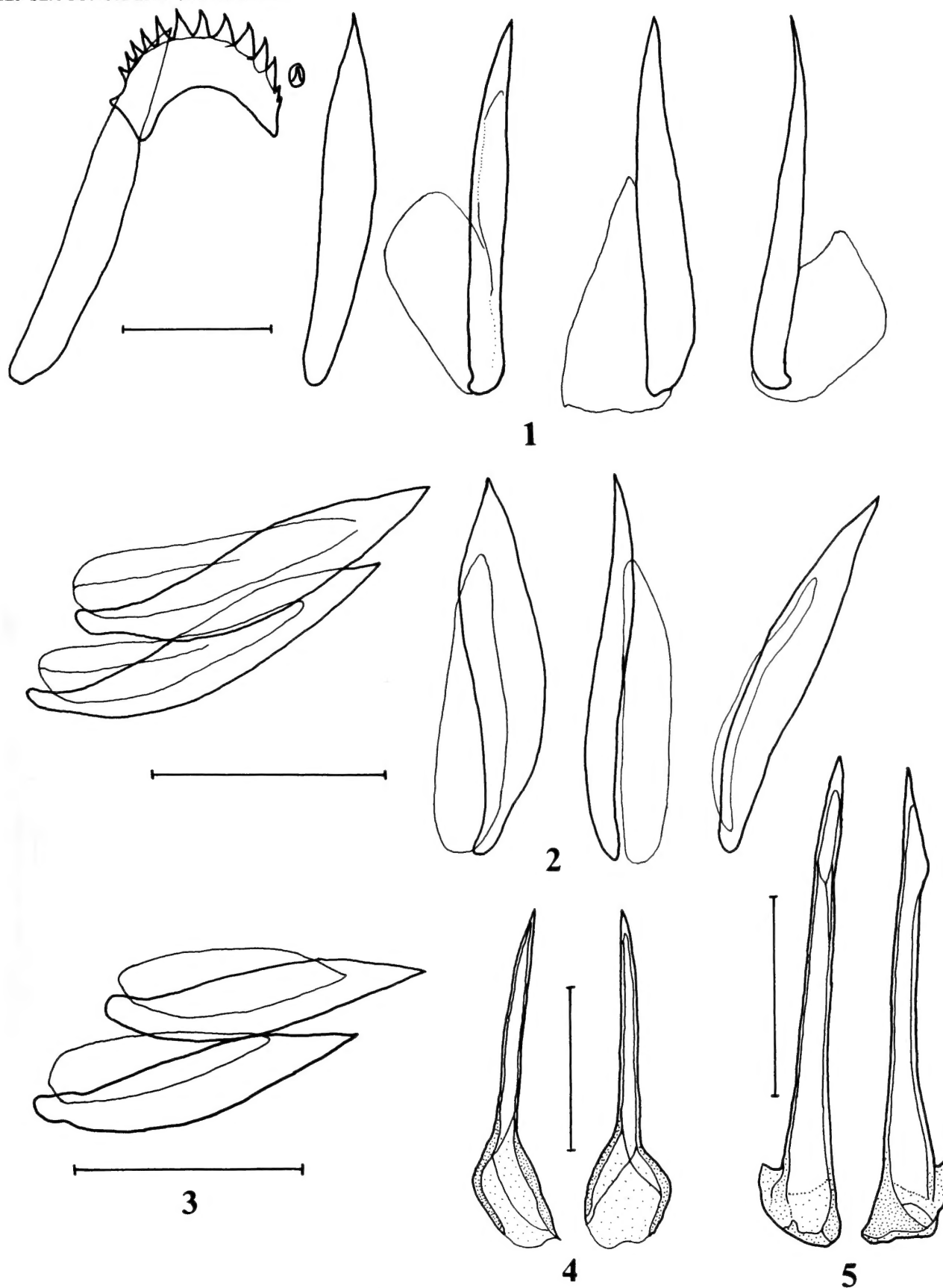
All the JME shells, unlike the specimens illustrated elsewhere, are uniformly coloured; the colour has probably faded since the

time of collection. The protoconch consists of about 2.5 whorls, with very small and adpressed initial volution. This is more than in the holotype (Shuto, 1975, pl. 6, fig. 17; though it is impossible to evaluate the exact number of volutions from the lateral side of the illustrated shell) and in Pleistocene shells (1 2/3 whorls, Shuto, 1965).

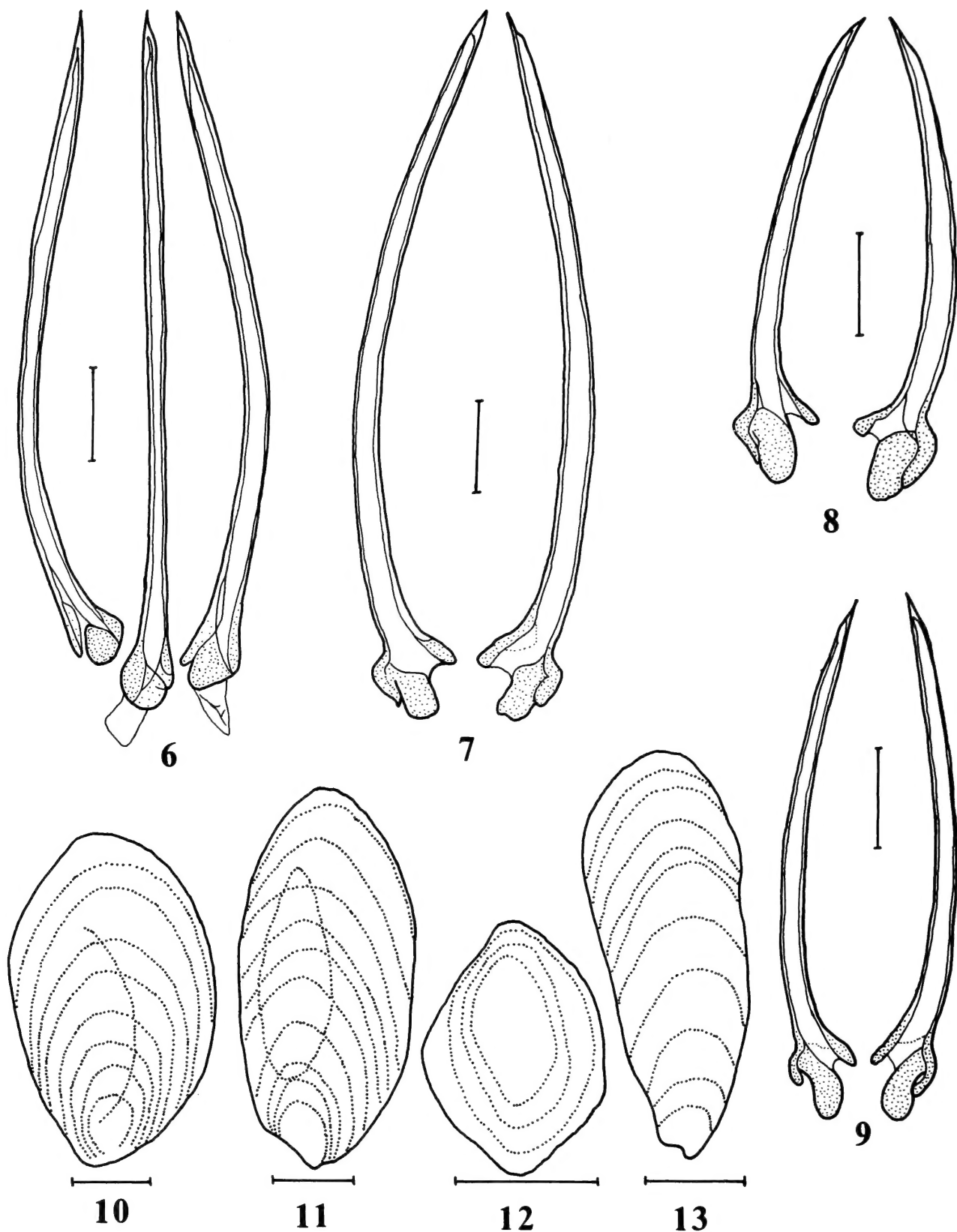
The JME shells are more similar to Japanese shells than to the geographically closer *H. madurensis* (Schepman, 1913). The latter species has somewhat broader and much smaller shell (holotype is 14.8 mm in height at 8 teleoconch whorls, according to Shuto, 1970, vs. 27.8–32.8 mm at 8–9 whorls in the JME shells) with shorter canal and weaker ribs. However in fact these species differ only slightly from each other, and *H. madurensis* seems to have no more than subspecific status.

The familial position of *Horaiclavus* is still uncertain. Its radula was never figured, though Oyama (Taki & Oyama, 1954) mentioned that it is similar to that of *Comitas* and *Inquisitor*. Shuto (1983) described the radula of *Horaiclavus* as 'true toxoglossate according to Kuroda, Habe and Oyama (1971, p. 327)'. However, the cited page contains no information about this genus. Until the examination of the radula, I have to follow Shuto (1975, 1983) in assigning *Horaiclavus* to Drilliidae.

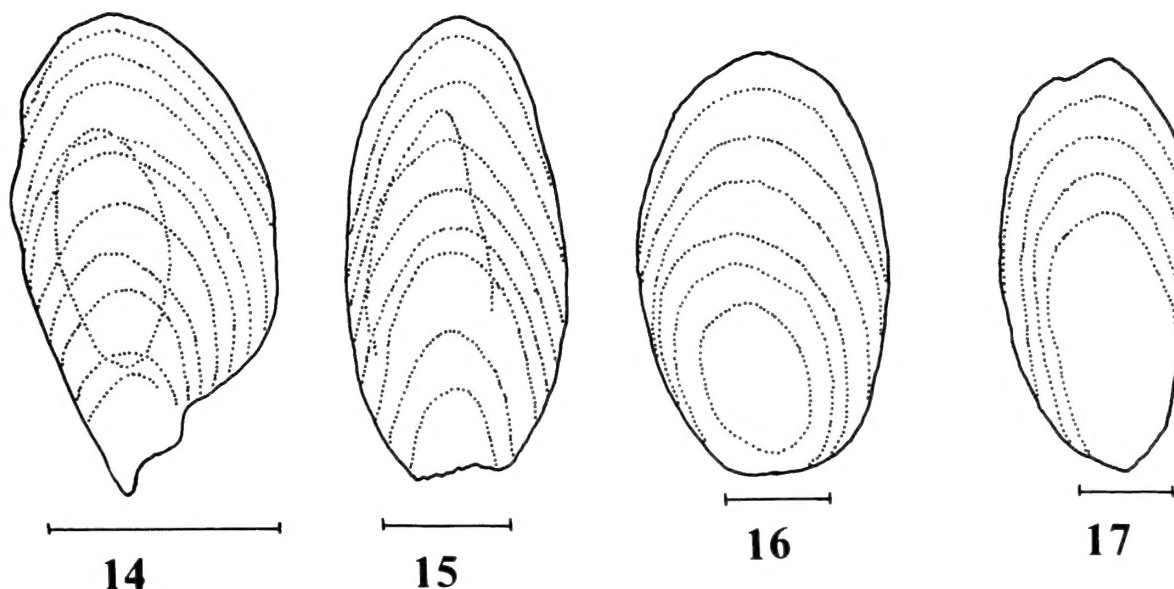
DISTRIBUTION. Japan, 50–200 m, and Gulf of Aden, 528–732 m. The present record is a considerable geographic as well as bathymetric range extension for the species.



Figs 1–5 Radulae. **1** – *Splendrillia zanzibarica* Sysoev, new species, holotype; **2** – *Inquisitor adenicus* Sysoev, new species, paratype, stn 33, H = 34.4 mm; **3** – *I. indistinctus* Sysoev, new species, paratype, stn 145, H = 27.4 mm; **4** – *Typhlomangelia adenica* Sysoev, new species, paratype, stn 185, H = 7.7 mm; **5** – *Borsonia (Cordieria) symbiophora* Sysoev, new species, paratype, stn 185, H = 21.8 mm. Scale-line = 0.1 mm.



Figs 6–13 Radulae (6–9) and opercula (10–13). **6** – *Typhlomangelia maldivica* Sysoev, new species, paratype, stn 143, H = 27.8 mm; **7** – *Bathytoma* (*Parabathytoma*) *oldhami* (E.A. Smith, 1899), stn 145, H = 41.0 mm; **8** – *B. (P.) regnans* Melvill, 1918, stn 34, H = 26.6 mm; **9** – *B. (P.) fissa* (von Martens, 1901), stn 176, H = 35.3 mm; **10** – *Splendrillia zanzibarica* Sysoev, new species, holotype; **11** – *Inquisitor indistinctus* Sysoev, new species, paratype, stn 145, H = 27.4 mm; **12, 13** – *Borsonia* (*Cordieria*) *symbiophora* Sysoev, new species, paratypes, stn 185, H = 21.8 mm (12) and stn 26, H = 20.1 mm (13). Scale-lines 0.1 mm (6–9) and 1 mm (10–13).



Figs 14–17 Opercula. **14** – *Typhlomangelia adenica* Sysoev, new species, paratype, stn 185, H = 7.7 mm; **15** – *T. maldivica* Sysoev, new species, paratype, stn 143, H = 27.8 mm; **16** – *Bathytoma* (*Parabathytoma*) *regnans* Melvill, 1918, stn 34, H = 26.6 mm; **17** – *B. (P.) fissa* (von Martens, 1901), stn 176, H = 35.3 mm. Scale-line = 0.1 mm.

Genus *SPLENDRILLIA* Hedley, 1922

Type species: *Drillia woodsi* Beddome, 1883 (original designation)

Splendrillia zanzibarica Sysoev, new species

Figs 1, 10 & 22

MATERIAL. stn 119, 1 specimen (holotype, No. 1993089) and 1 shell (paratype, No. 1993090).

DESCRIPTION OF HOLOTYPE. The shell is of medium size for the genus, slender, angularly claviform, grayish-white with dull surface, rather thin, consisting of 5.5 remained whorls. The protoconch is missing; the bluntly closed beginning of initial teleoconch whorls is seen in the shell apex. The whorls are angled slightly above the periphery, concave above the angulation and almost flat below it. Sutures are clear, shallow, slightly wavy. The spire is high, occupying about 0.4 of the shell height. Axial sculpture consists of strong oblique folds, rapidly disappearing on subsutural slope and forming pointed tubercles at the whorl periphery. Intervals between folds are narrower than the folds themselves. The folds reach the lower part of the shell base but weaken greatly on the last third of the body whorl. There are about 15 folds on the body whorl and 12 on the penultimate. Spiral sculpture is absent except for very indistinct striation seen only on the shell base near aperture. The aperture is oval and gradually narrows towards the canal. The inner lip is covered by a longitudinally rugose callus. The anal sinus is rather shallow, broadly open, with the edge somewhat spout-like. The canal is moderately long and wide. H = 19.3, Hb = 11.7, Ha = 9.3, D = 8.1 mm.

The operculum is oblanceolate, with a terminal nucleus. Radula is typical for the genus, with small central and comb-like lateral teeth. Each marginal tooth is accompanied by a transparent, usually more or less triangular plate at its base (better seen in detached teeth) which is probably a part of

radular membrane serving as a tooth ligament. Mean length of marginal teeth is 0.26 mm.

The shell of the paratype (H = 19.4 mm) is badly worn and does not differ from the holotype in essential characters.

The species is characterized by strongly angled whorls, oblique axials, and, especially, long canal. It resembles the East African *Drillia indra* Thiele, 1925 while differing in having almost 3 times larger shell with long axials and without a distinct angulation at the shell base.

DISTRIBUTION. Zanzibar, 1207–1463 m.

Family *TURRIDAE* H. & A. Adams, 1853

Subfamily *CLAVATULINAE*

Genus *TURRICULA* Schumacher, 1817

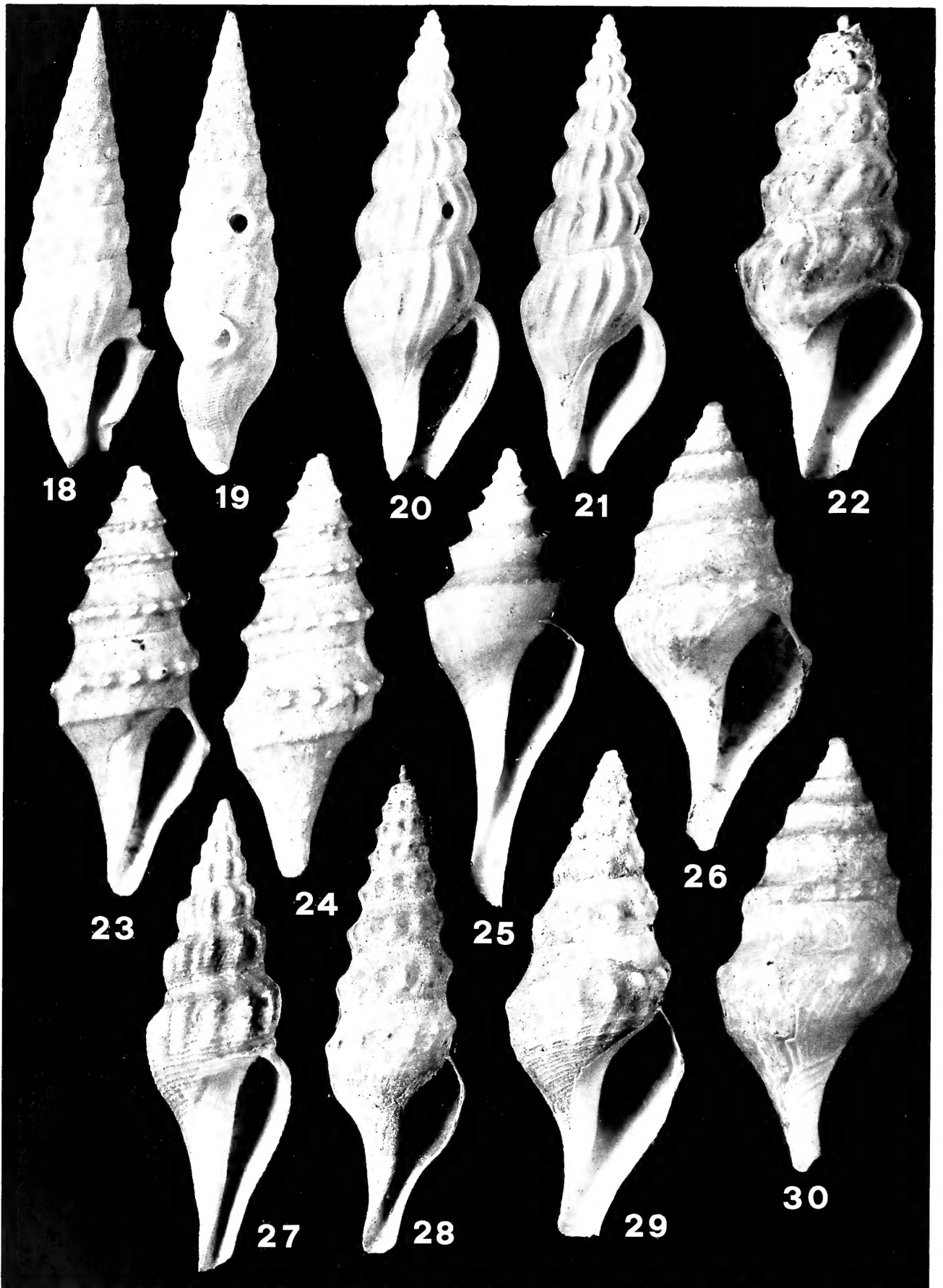
Type species: *Turricula flammea* Schumacher, 1817 (monotypy) (= *Murex tornatus* Dillwyn, 1817)

Turricula new species

Figs 26 & 30

MATERIAL. stn 119, 1 shell.

A single young shell (H = 21.0 mm) apparently represents a new species. It resembles most closely the shallow-water species *Turricula catena* (Reeve, 1843) distributed in the Red Sea and Persian Gulf, but clearly differs in the absence of the subsutural fold sculptured with axial ribs and in the absence of spiral sculpture on the shell base. In general shell outline it also resembles *Surcula fulminata* var. *gloriosa* Melvill, 1917, which Powell (1969) dismissed as an abnormal variant of *Turricula tornata fulminata* (Kiener, 1839–40), but is distinguished in its heavy nodulose peripheral carina and almost complete absence of spiral ribs except for those on the canal. However it seems



reasonable to refrain from formal description of a new species based on a single young shell.

DISTRIBUTION. Zanzibar, 1207–1463 m.

Subfamily **COCHLESPIRINAE** Powell, 1942

Genus **COCHLESPIRA** Conrad, 1865

Type species: *Pleurotoma cristata* Conrad, 1847 (monotypy)

***Cochlespira travancorica* (E.A.Smith, 1896)**

Fig. 25

Pleurotoma (*Ancistrosyrinx*) *travancorica* E.A.Smith, 1896, p. 368; 1906, p. 163; Alcock & Anderson, 1898, pl. 7, figs 1, 1a.

Pleurotoma (*Ancistrosyrinx*) *travancorica* var. *granulata* E.A.Smith, 1904, p. 459.

Ancistrosyrinx *travancorica* var. *granulata* (E.A.Smith) – Schepman, 1913, p. 420.

Cochlespira *travancorica* *travancorica* (E.A.Smith) & *C. travancorica* *travancorica* forma *granulata* (E.A.Smith) – Powell, 1969, p. 396–397, pl. 307.

TYPE LOCALITY. off Travancore (India), 460 fms (*travancorica*), ‘Investigator’, stn 229, 360 fms (var. *granulata*).

MATERIAL. stn 107, 1 shell.

The JME specimen was determined and described by Powell (1969: 396–397) as *C. travancorica* *travancorica* forma *granulata*. However this specimen differs from the latter variety (in accordance with both original and Schepman’s (1913: 420) descriptions) in the absence of granules on the spiral ribs of the shell base and subsutural slope. The only character in common with the variety *granulata*, is the presence of weak spiral ribs on the subsutural slope. At the same time, these differences are taxonomically insignificant since the variety *granulata*, as it was mentioned by Powell, apparently does not warrant even a subspecific status and represents a form of intraspecific variability (this, in particular, makes superfluous the recognition of the nominotypical subspecies by Powell (1969: 396)).

DISTRIBUTION. East Africa, India, Indonesia, 338–743 m.

***Cochlespira zanzibarica* Sysoev, new species**

Figs 23 & 24

MATERIAL. stn 119, 1 shell (holotype, No. 1993091).

DESCRIPTION. The shell is small, light-brown, with glossy surface, rather solid, fusiform, consisting of 6.5 preserved whorls. The protoconch is missing and the upper whorls are heavily eroded. The whorls are angled below the periphery and concave upper and below the angulation; the position of the angulation on the spire whorls shifts upward towards the body whorl. The sutures are straight and very shallowly impressed. The sculpture consists only of a strong median keel with rounded, pointed tubercles (16 on the body and penultimate

whorls) and a low ridge on the upper part of the shell base. The ridge is hard to trace above the suture on last spire whorls. The growth lines are very thin. The shell base is angled in its upper part, where the ridge is situated, and slightly and evenly concave below the angulation; it smoothly passes into the canal. The aperture is narrow, with the inner lip weakly and evenly curved. The anal sinus is broad and moderately deep, with the apex situated in the middle of subsutural slope. The canal is straight and rather short (the end is apparently slightly broken). H = 16.9, Hb = 10.2, Ha = 7.6, D = 6.9 mm.

The new species obviously belongs to the ‘*semitiplana* group’ sensu Powell, 1969 which includes two fossil and two Recent deep-water species and is characterized by the presence of a strong basal keel. The new species differs from all known species of the group by the complete absence of spiral sculpture on the shell base, except for low ridge and in its more stout shell with rather short canal. It is also similar to species of the genus *Chesasyrinx* Petuch, 1988 known from Miocene of Maryland, USA. Although Petuch (1988: p. 38–39) did not compare *Chesasyrinx* with *Cochlespira* in the original description, the striking similarity of shells of *Chesasyrinx* and ‘*semitiplana* group’ of *Cochlespira* may be reason for synonymizing these genera.

DISTRIBUTION. Zanzibar area, 1207–1463 m.

Genus **COMITAS** Finlay, 1926

Type species: *Drillia fusiformis* Hutton, 1877 (= *Surcula huttoni* Suter, 1914) (original designation)

***Comitas subsuturalis* (von Martens, 1902)**

Figs 31–40

Pleurotoma (*Brachytoma*) *subsuturalis* von Martens, 1902, p. 239.

Brachytoma *subsuturalis* (von Martens) — von Martens, 1903 [1904], p. 85, pl. 1, fig. 7.

Comitas *subsuturalis* (von Martens) — Powell, 1969, p. 285, pl. 226, figs 3–4.

TYPE LOCALITY. ‘Valdivia’, stn 256, off Somali, 1134 m.

MATERIAL. stn 33, 3 specimens and 4 shells; stn 34, 1 specimen and 8 shells; stn 118, 1 specimen and 1 shell; stn 143, 9 specimens; stn 145, 2 specimens; stn 184, 7 specimens and 1 shell; stn 193, 3 shells.

Examination of the large series of JME specimens revealed very a high variability of *C. subsuturalis* in sculpture and shell proportions. Some specimens are very similar to the original illustration of von Martens (e.g. Figs 37, 38) whilst others, often from the same station, may differ in narrower (or, conversely, broader) shells with more or less high position of peripheral keel, variously differentiated spiral ribs on the shell base, and more or less prominent and numerous tubercles on subsutural fold. The largest JME shell is 32.4 mm in height and 12.0 mm in width.

Figs 18–30 Clavusidae, Clavatulinae and Cochlespirinae. **18, 19** – *Drillia altispira* Sysoev, new species, holotype; **20, 21** – *Horaiclavus splendidus* (A. Adams, 1867), stn 188 (**20**) and 176 (**21**), H = 32.4 (**20**) and 32.8 (**21**) mm; **22** – *Splendrilla zanzibarica* Sysoev, new species, holotype; **23, 24** – *Cochlespira zanzibarica* Sysoev, new species, holotype; **25** – *Cochlespira travancorica* (E.A. Smith, 1896), stn 107, H = 19.1 mm; **26, 30** – *Turricula* new species, stn 119, H = 21.0 mm; **27** – *Comitas elegans* Sysoev, new species, holotype; **28** – *Leucosyrinx claviforma* (Kosuge, 1992), stn 158, H = 28.0 mm; **29** – *Comitas curvuplicata* Sysoev, new species, holotype.

Powell (1969, p. 285) mentioned 'a related new species from the Gulf of Aden in 1270 metres', i.e. from stn 184, but did not give a formal description nor reasons for this. However, extreme variants of *C. subsuturalis* from stn 184 are connected by intermediate forms and can be therefore identified as that species.

Specimens from two stations off Maldive Islands comprise a distinct group differing from East African shells in smaller size (15.5–21.0 mm at 6–7 teleoconch whorls vs. 21.8–28.7 in typical *C. subsuturalis*) and more slender shell proportions (H/D ratio is 2.82–3.12, mean 2.95 ($n = 11$) vs. 2.10–2.94 (2.10–2.70 in 19 out of 20 shells measured), mean 2.34). These differences are probably connected with geographical isolation of the Maldive Islands resulting in formation of morphologically isolated population of the species. If the above-mentioned metric differences will be confirmed in additional samples, the population of *C. subsuturalis* from Maldive Islands should be considered as a distinct subspecies. This population represents a transition (both geographical and conchological) to *C. exstructa* von Martens, 1903, described from Nicobar Islands. The latter species is distinguished only by an even narrower shell (H/D ratio is 3.43 in the holotype) with longer axial folds (as far as it can be judged from von Martens' figure). Examination of type material may however reveal that *C. exstructa* is a synonym of *C. subsuturalis*. A similar statement is probably true for *C. obtusigemmata* Schepman, 1913, which does not differ from *C. subsuturalis* in essential conchological characters.

DISTRIBUTION. East Africa from the Gulf of Aden to Zanzibar, and Maldive Islands, 494–1789 m.

Comitas erica (Thiele, 1925)

Fig. 41

Leucosyrinx erica Thiele, 1925, p. 236, pl. 36(24), fig. 25.

Comitas erica (Thiele) — Powell, 1969, p. 284, p. 226, fig. 2.

TYPE LOCALITY. 'Valdivia', stn 191, off Siberut Id. (Sumatra), 750 m.

MATERIAL. stn 143, 2 specimens. Also mentioned by Powell (1969) from stn 108 (Zanzibar area, SE of Pemba Island, 786 m).

Both specimens are very similar to the original figure and the species variability thus seems to be rather low. One of JME specimens is larger than Thiele's holotype (20.9 vs. 16.5 mm), but has the appearance of an immature shell. The species was found in the sample also containing *C. subsuturalis*, but it can be easily distinguished from the latter, by the grayish-white shell with weaker subsutural tubercles, closer-spaced spiral ribs, two of which on the upper shell base are more prominent, and larger protoconch (0.95 mm in diameter vs. 0.7–0.8 mm in *C. subsuturalis* from the same sample).

DISTRIBUTION. Sumatra, Zanzibar and Maldive Islands, 750–797 m.

Comitas paupera (Watson, 1881)

Figs 42–48

Pleurotoma (*Drillia*) *paupera* Watson, 1881, p. 411.

Pleurotoma (*Typhlomangelia*) *paupera* Watson – Watson, 1886, p. 317–319, pl. 25, fig. 3.

Turricula paupera Watson – Powell, 1969, p. 244, pl. 202.

TYPE LOCALITY. 'Challenger', stn 191, off the Arrou Islands (Arafura Sea, Indonesia), 800 fms.

MATERIAL. stn 62, 2 specimens; stn 185, 3 specimens and 4 shells.

Proper determination of this species is rather intricate due to the very heterogeneous type material. Powell (1969) erroneously described Watson's syntypes as consisting of two shells with rounded lower whorls and obsolescent sculpture and one shell angulate with strong axially costae. He illustrated the latter specimen and designated it as the holotype (correctly named lectotype in the 'Measurement' and 'Types' paragraphs). Actually, one of the two paralectotypes ($H = 33.3$ mm) has a rounded body whorl with obsolete axials while the axial sculpture on spire whorls is almost the same as in the lectotype (Figs 42 & 43). The second paralectotype (Fig. 44) is represented by a small ($H = 18.5$ mm) and quite dissimilar shell, characterized by strongly angled whorls with axial sculpture consisting of strong and rounded tubercles at the place of whorl angulation. This specimen is so distinct that one could easily assign it to a separate species if it was not found in the same sample.

Two at first glance rather different shells from the JME stn 62 fit however in the range of variability described above. The larger shell ($H = 23.4$ mm, Fig. 45) is comparable to the lectotype, but has less convex whorls with a less pronounced subsutural slope. The smaller shell ($H = 17.5$ mm, Fig. 46) is very similar to the smaller paralectotype, but has even stronger peripheral nodules. Small specimens (14–15 mm in height) from stn 185 (Figs 47 & 48) have shells and sculpture intermediate between the extreme variants. In some of the latter specimens, the spiral ribs are more widely spaced on the shell base and reduced in number on the subsutural slope.

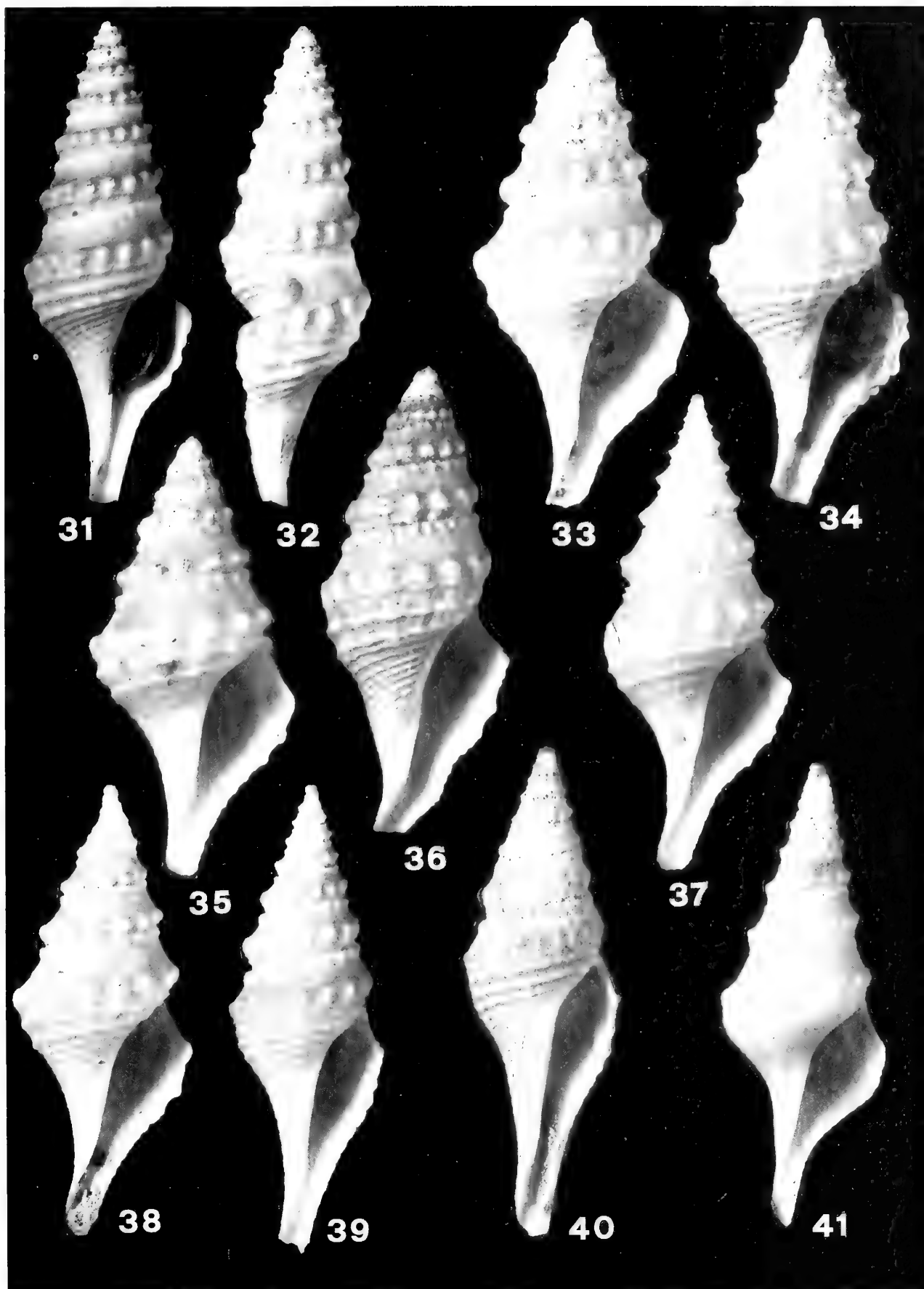
Thus, *C. paupera* appears to be very variable species with extreme variants being quite dissimilar to each other but connected by intermediate forms.

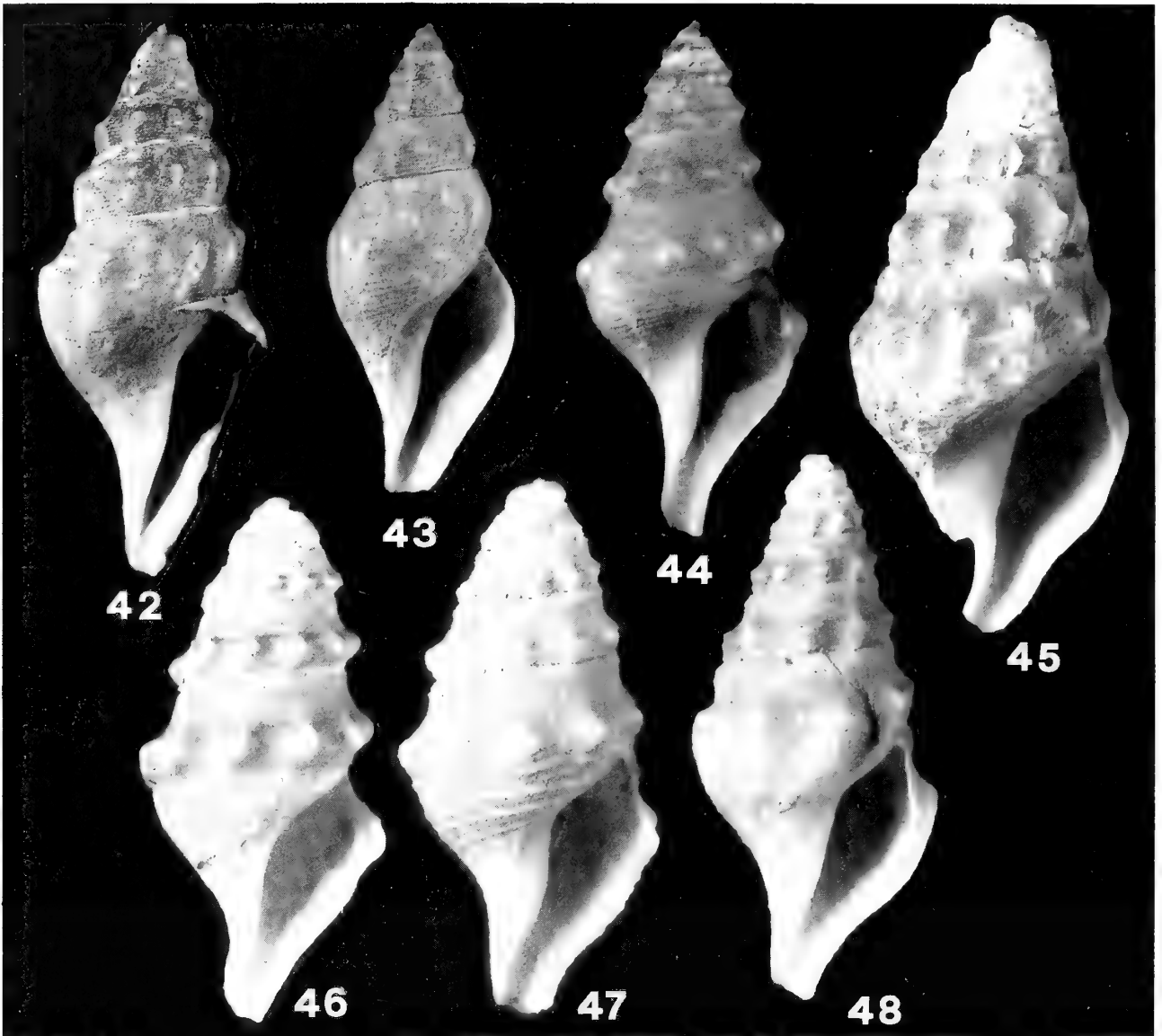
The species was included by Powell (1969) into the genus *Turricula* Schumacher, 1817. However its operculum has a terminal nucleus characteristic of the genus *Comitas*.

Surcula suratensis Thiele, 1925 (= *Surcula coreanica* of von Martens, 1903, not of Adams & Reeve, 1850) is similar to some forms of *C. paupera* and after examination of type material it may appear to be a synonym of the latter.

DISTRIBUTION. Indonesia, Gulf of Aden, and Gulf of Oman, 1463–2000 m.

Figs 31–41 *Comitas subsuturalis* (von Martens, 1902) (31–40) and *C. erica* (Thiele, 1925) (41). 31, 32 – stn 184, $H = 37.3$ mm; 33 – stn 184, $H = 25.5$ mm; 34 – stn 184, $H = 24.0$ mm; 35 – stn 33, $H = 21.0$ mm; 36 – stn 184, $H = 28.6$ mm; 37 – stn 34, $H = 27.0$ mm; 38 – stn 184, $H = 21.7$ mm; 39 – stn 143, $H = 21.0$ mm; 40 – stn 145, $H = 26.2$ mm; 41 – stn 143, $H = 20.9$ mm.





Figs 42–48 *Comitas paupera* (Watson, 1881). **41** – lectotype, H = 40.0 mm; **43, 44** – paralectotypes, H = 33.3 (43) and 18.5 (44) mm, BM(NH) 1887.2.9.1009 11; **45, 46** – stn 62, H = 23.4 (45) and 17.5 (46) mm; **47, 48** – stn 185, H = 14.0 (47) and 14.9 (48) mm.

***Comitas curvuplicata* Sysoev, new species**

Fig. 29

MATERIAL. stn 184, 2 specimens (holotype No. 1993092 and paratype No. 1993093).

DESCRIPTION OF HOLOTYPE. The shell medium size, fusiform, rather thin, covered with light-brown periostracum, consists of 7 whorls. The protoconch is missing. The whorls are angled at the periphery or below it (on upper whorls). The subsutural slope is broad and weakly concave. Sutures are slightly wavy, shallow. Axial folds are low, reversed-sigmoid, they form strong rounded nodules below the subsutural slope and then rapidly weaken and become narrowly crested, but extend to the lower suture on the spire whorl and to lower part of the shell base. There are 15 axial folds on the body whorl and 13 on the penultimate. The subsutural slope is devoid of axial sculpture. Growth lines are mostly indistinct except those on the subsutural slope, but some are rough and raised. Spiral ribs are unequal in width and

prominence, generally they are most closely spaced in intervals between peripheral nodules and further apart on the lower shell base and the canal. Two ribs on the upper shell base are raised and most prominent. The subsutural slope is covered with subobsolete, closely set ribs which are obsolete on some parts of the shell; there are also two shallow grooves in the middle of subsutural slope. The body whorl is large, occupying about 0.66 of the shell height. The shell base is almost flat, evenly curved in transition to the canal. The aperture is oval, with the inner lip evenly curved and covered by a wide callus which bears oblique folds being the continuation of spiral ribs. The anal sinus is moderately deep, broadly V-shaped, with its apex being in the middle of subsutural slope. The canal is moderately long, slightly turned to left. The operculum is large, leaf-shaped, with terminal nucleus. H = 32.4, Hb = 21.6, Ha = 17.6, D = 13.0 mm.

The paratype (H = 29.2, D = 11.8 mm) is similar to the holotype, but has rather worn surface.

The new species is similar to *C. arcana* (E.A. Smith, 1899) from Andaman Islands and Southern India (338–658 m) but differs in

having a slightly larger shell with shorter and broader canal, shorter spire (its height is less than that of aperture plus canal), and long axials with characteristic reversed-sigmoid curvature and less strong and more numerous nodules.

DISTRIBUTION. Gulf of Aden, 1270 m.

***Comitas elegans* Sysoev, new species**

Fig. 27

MATERIAL. stn 176, 1 shell (holotype, No. 1993094).

DESCRIPTION. The shell is medium size, fusiform, slender, with a high turreted spire, solid, white under a grayish-brown periostracum, and consists of 8 whorls. The protoconch is missing. Whorls are roundly angled at the shoulder, with conspicuous subsutural fold, slightly concave subsutural slope, and almost vertical lateral sides. Sutures are shallow, wavy, and slightly channelled. Axial folds (12 on the body whorl and 11 on the penultimate one) are strong, oblique, broad, and rounded. They rapidly disappear on subsutural slope and slightly weaken towards the lower suture. On the body whorl, the folds are present on the whorl periphery and fade on the upper part of the shell base. Intervals between folds are narrower than the folds themselves. Spiral ribs are low, broad, rounded and divided by narrow interstices in the upper part of whorls below the subsutural slope. Towards the lower suture and on the shell base they become narrower, thread-like, and more widely spaced. Subsutural slope is smooth except for indistinct spiral grooves in the middle. Growth lines are numerous, thin, prominent on the subsutural slope. The shell base is almost flat; weakly curving, it passes smoothly into a long and straight canal. The aperture is narrow, elongate-oval and not differentiated from the canal. The inner lip is almost straight along most of its length, covered by wide but thin callus. The anal sinus, judging from growth lines, is rather deep, V-shaped, with the apex situated just below the middle of subsutural slope. $H = 38.3$, $H_b = 24.7$, $H_a = 19.0$, $D = 11.6$ mm.

The new species is very similar to *Drillia investigatoris* E.A.Smith, 1899 and differs in having a much smaller shell (65 mm in the unique holotype of *D. investigatoris*) with subsutural slope devoid of spiral sculpture.

DISTRIBUTION. Gulf of Aden, 655–732 m.

***Comitas* sp.**

MATERIAL. stn 184, 1 shell.

A single broken shell ($H = 24.4$, upper spire whorls missing) is rather similar to *C. trailli* (Hutton, 1873) from New Zealand, but the worn condition of the shell hampers its proper identification.

Genus *LEUCOSYRINX* Dall, 1889

TYPE SPECIES. *Pleurotoma verrilli* Dall, 1881 (original designation)

***Leucosyrinx claviforma* (Kosuge, 1992)**

Fig. 28

Comitas claviforma Kosuge, 1992, p. 165–166, pl. 58, figs 7–8.

TYPE LOCALITY. off Port Hedland, Western Australia, 376 m.

MATERIAL. stn 158, 1 shell.

The JME shell differs from the unique holotype in having slightly less angled whorls, lower spire (though the shell is smaller: $H = 28.0$ mm vs. 38.1 mm in the holotype), and reddish brown colour (ashy white in the holotype). However, all other conchological characters agree with original description and illustrations.

The species was described as *Comitas*, but the narrow, turreted shell with angled whorls and the anal sinus scars indicating a deep sinus with greatly projected outer lip are more typical of the genus *Leucosyrinx*.

DISTRIBUTION. Western Australia and Maldive Islands, 376–1170 m.

Subfamily **CRASSISPIRINAE** Morrison, 1966

Genus *INQUISITOR* Hedley, 1918

Type species: *Pleurotoma sterrha* Watson, 1881 (original designation)

***Inquisitor nodicostatus* Kilburn, 1988**

Fig. 49

Crassispira aesopus (non Schepman, 1913) – Kilburn, 1973, p. 572, fig. 13a.

Inquisitor nodicostatus Kilburn, 1988, p. 259–261, figs 36, 42, 213–214.

TYPE LOCALITY. Natal, South Africa (29°43'S, 31°05'E), 164–169 fms.

MATERIAL. stn 106, 1 shell.

DISTRIBUTION. South Africa and Zanzibar, 183–310 m.

***Inquisitor adenicus* Sysoev, new species**

Figs 2 & 50–53

MATERIAL. stn 33, 1 paratype No. 1993096/1; stn 34, 7 paratypes No. 1993096/2–8; stn 193, holotype No. 1993095 and 4 paratypes No. 1993096/9–12.

DESCRIPTION OF HOLOTYPE. The shell is medium sized for the genus, claviform, thin but solid, with a high spire, covered with olivaceous-brown periostracum, and consisting of 8 whorls. The protoconch is missing and the upper whorls are eroded. Whorls are obtusely angled at the shoulder and moderately convex. Subsutural slope is broad and concave and the subsutural fold is weak and indistinct. Sutures are shallow and wavy. Axial folds are strong and rounded, slightly oblique, with interstices narrower than folds. Folds extend from the lower suture to the lower part of subsutural slope where they rapidly disappear. There are ten folds on each of two last whorls. Growth lines are thin, prominent on the subsutural slope. Spiral cords are strong, rounded, almost equally developed on axial folds and in interstices; they are much narrower than the interspaces between them. The cords are absent on subsutural slope and become narrower, closer and much weaker on lower part of the shell base towards the canal end. There are four cords on the spire whorls (five on the penultimate one, the lowest cord submargins the suture), five on the body whorl periphery, and, below a wider interval, about 12 on the shell base and canal. The aperture is elongate-oval, rather narrow, becoming slightly narrower as it passing into the canal. Outer lip with thin edge; inner lip

concave, covered with wide, longitudinally rugose callus, which does not form a pad at the sinus entrance. The anal sinus is deep, narrows markedly towards the apex, U-shaped (type (c) of Kilburn, 1988), and its deepest point is situated slightly below the middle of subsutural slope. The canal is moderately long and straight. $H = 33.0$, $H_b = 18.4$, $H_a = 13.8$, $D = 10.3$ mm.

The paratypes vary slightly in the character of spiral sculpture: the cords may be unevenly spaced, rarely with thinner additional cords in some intervals. The subsutural fold is variously developed, sometimes it is distinct. The canal is narrower and sometimes curved in smaller shells and broader and therefore visually shorter in larger paratypes. The largest paratype is 34.3 mm in height.

In the only paratype with an intact protoconch, it consists of 1.5 rapidly increasing globose whorls (1.0 mm in diameter) with a smooth surface. An operculum was not found; it might be lost in the dried animal. The radula (Fig. 2) is typical of the genus, teeth with tapering distal end of the shaft, poorly differentiated cutting edge, and large and broad accessory limb. The tooth length is 0.17 mm (in paratype from stn 33, $H = 34.3$ mm).

The new species resembles *Funa laterculoides* (Barnard, 1958) in general outlines but clearly differs in its protoconch, colour, radula, and details of sculpture.

DISTRIBUTION. Gulf of Aden, 1022–1295 m.

Inquisitor indistinctus Sysoev, new species

Figs 3, 11 & 54–55

MATERIAL. stn 145, 3 specimens and 1 shell (holotype No. 1993097 and 3 paratypes No. 1993098).

DESCRIPTION OF HOLOTYPE. The shell is medium size, claviform, slender, with rather high spire, thin but solid, covered with solid olivaceous periostracum, and consists of protoconch and 9 teleoconch whorls. The protoconch is small (0.95 mm in diameter) consisting of 1.5 smooth glossy whorls. Definitive whorls weakly convex, with a slight angulation at the shoulder. Subsutural slope concave except for weak subsutural fold. Sutures straight, moderately deep, become slightly channelled on the body whorl. The axial sculpture is represented by strong oblique rounded folds, gradually disappearing on subsutural slope and reaching the lower suture or, on the body whorl, the shell base. The folds tend to weaken on the last half of the body whorl. There are 14 folds on the body and penultimate whorls. Spiral cords override the axial folds, they are low, wide and rounded, the intervals are approximately equal to cords in width or somewhat wider. There are 16 cords on the body whorl and 7–8 on the penultimate. The shell base is weakly convex, and smoothly passes into the canal. The aperture is rather narrow, elongate-oval, and not differentiated from the canal. The latter is short and wide, somewhat expanded and shallowly notched at the end. The anal sinus is moderately deep, rounded, symmetrical, and occupies the entire subsutural slope. The inner lip is covered with thick white callus with a free edge in the lower part. Columella almost straight. $H = 31.3$, $H_b = 16.5$, $H_a = 12.4$, $D = 8.3$ mm.

The paratypes are smaller (H no more than 27.4 mm) and vary slightly in the prominence of the axial and spiral sculpture

including the subsutural fold. In one paratype, there is a weak but distinct callus pad at the entrance to anal sinus. The operculum is oblongate, with terminal nucleus. Marginal teeth of the radula possess broad leaf-shaped accessory limb, which does not reach the distal end of the shaft. The mean tooth length is 0.14 mm (in paratype with $H = 27.4$ mm).

DISTRIBUTION. Maldives Islands, 494 m.

Inquisitor stenosis Sysoev, new species

Figs 56 & 57

MATERIAL. stn 176, 1 shell (holotype, No. 1993099).

DESCRIPTION. The shell is rather small, slender, with high spire comprising about 0.5 of the shell height, yellowish-white, and consisting of 9 whorls. The protoconch is missing. Whorls are strongly angled at the periphery, and the whorl profile is very weakly concave above the angulation and almost flat below it. There is a narrow and weak subsutural fold. Sutures are straight and moderately deep. The axial sculpture consists of slightly oblique and widely spaced folds (9 on each of two last whorls) forming longitudinally elongated and sometimes pointed strong tubercles in the middle of the whorl. On early spire whorls, the folds are obsolete but visible on the lower part of subsutural slope and reach the lower suture. Towards the body whorl, they become obsolete near the lower suture and over most part of subsutural slope, but again become longer and extend over entire shell base in the last half of the body whorl. The last fold situated behind the aperture edge is much wider and stronger than other. Spiral sculpture consists of indistinct, rather broad ribs which are obsolete or subobsolete in interstices between axial folds and absent on the subsutural slope. The aperture is narrow, elongate-oval, with a thick labial callus and straight columella. The labrum has a thin edge and low and narrow fold-like varix behind the edge. The anal sinus is moderately deep, U-shaped, with slightly constricted entrance (type (b) of Kilburn, 1988). There is a moderately large, pointed, and outwardly projecting parietal tubercle. $H = 21.3$, $H_b = 10.7$, $H_a = 18.4$, $D = 5.7$ mm.

The new species is distinguished by its small narrow shell with high spire, broad subsutural slope, low but strongly tuberculated at the periphery axial folds, and obscure spiral ribs.

DISTRIBUTION. Gulf of Aden, 655–732 m.

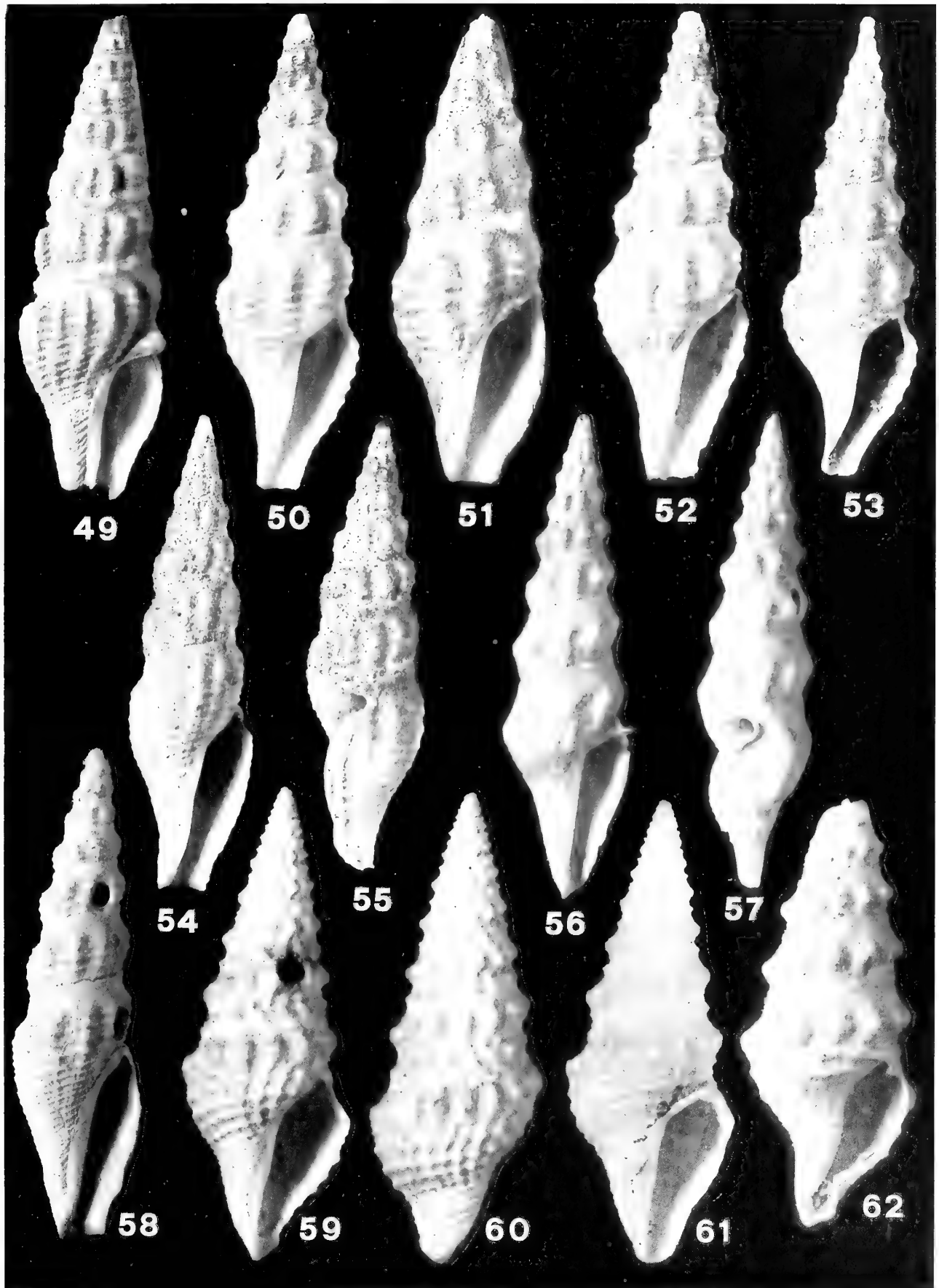
Inquisitor angustiliratus Sysoev, new species

Fig. 58

MATERIAL. stn 188, 1 shell (holotype, No. 1993100).

DESCRIPTION. The shell is moderately large, with a rather high spire, strong, yellowish-gray, and consisting of 8 whorls. The protoconch is missing. Whorls are moderately convex, slightly angled at the shoulder, with indistinct subsutural fold and moderately wide (about 1/3 of the whorl height), concave subsutural slope. Sutures are wavy, and slightly channelled. Axial folds (12 on the body whorl and 11 on the penultimate one) are narrow, slightly oblique, with sharpened crests, and long (they reach the lower suture and extend over the entire shell base). The folds begin in the lower part of the subsutural slope

Figs 49–62 Crassispirinae. **49** – *Inquisitor nodicostatus* Kilburn, 1988, stn 106, $H = 36.8$ mm; **50–53** – *I. adenicus* Sysoev, new species, holotype (**50**) and paratypes, stn 33 (**51**) and 34 (**52–53**), $H = 34.3$ (**51**), 30.9 (**52**) and 26.3 (**53**) mm; **54, 55** – *I. indistinctus* Sysoev, new species, holotype (**54**) and paratype, stn 145, $H = 26.0$ mm (**55**); **56, 57** – *I. stenosis* Sysoev, new species, holotype; **58** – *I. angustilirata* Sysoev, new species, holotype; **59, 60** – *Paradrillia agalma* (E.A. Smith, = 1906), stn 176, $H = 15.3$ mm; **61** – *P. agalma*?, stn 180, $H = 14.4$ mm; **62** – *Ceritoturris* sp., stn 42, $H = 11.8$ mm.



and are most prominent in the whorl periphery. Spiral ribs are strong, cord-like, narrow, widely spaced (but become progressively closer to each other and lower on the shell base and canal); they override the axial folds and form nodules at intersections. Interspaces between ribs are very finely spirally striate and sometimes bear a thin thread. The number of ribs increases from 3 to 5 in successive spire whorls. The subsutural fold is sculptured by two thin spiral riblets. Subsutural slope is smooth except for very fine spiral striations and 3–4 thin threads in the lower half. Growth lines are numerous, thin, and clear, on the body whorl some of them are rough and raised. The shell base is almost flat and not differentiated from the canal. The aperture seems to be rather wide (the outer lip is broken). The inner lip is weakly and evenly curved, and covered by thick callus. The parietal callus pad is very weak. The anal sinus (judging from its scars) is moderately deep, openly U-shaped (type (c) of Kilburn, 1988). The canal is broad and widely open. $H = 39.5$, $H_b = 21.4$, $H_a = 16.5$, $D = 10.8$ mm.

The new species resembles *I. coxi* (Angas, 1867) from south-eastern Australia in whorl outline and the character of sculpture but clearly differs in the shell proportions. It also looks somewhat like an extremely stretched out specimen of *I. crassa* (E.A.Smith, 1888).

DISTRIBUTION. Gulf of Aden, 528 m.

Genus *PARADRILLIA* Makiyama, 1940

Type species: *Drillia dainichiensis* Yokoyama, 1923 (original designation)

Paradrillia agalma (E.A.Smith, 1906)

Figs 59–61

Pleurotoma (*Surcula*) *agalma* E.A.Smith, 1906, p. 162–163; Annandale & Stewart, 1909, pl. 21, figs 4, 4a.

Paradrillia agalma (E.A.Smith) – Powell, 1969, p. 317, pl. 246, figs 1, 2.

TYPE LOCALITY. 'Investigator', stn 269, West of Cape Comorin (SE India), 464 fms.

MATERIAL. stn 176, 1 shell; stn 180, 2 shells.

The shell from stn 176 is quite typical. It consists of protoconch and 7 teleoconch whorls. The previously undescribed protoconch is basically similar to that of *P. melvilli* figured by Powell (1969, pl. 242, fig. 2). It consists of 2.5 whorls with smooth glossy surface, the tip is small and papillate, and a thin low-set keel is developed on the last whorl. There are 17 axial ribs on the body whorl and 15 on the penultimate one.

The shells from stn 180 (Fig. 61) were referred to *P. agalma* with some doubts. They differ in more numerous peripheral tubercles, weaker axial and spiral sculpture, and in the presence of two spiral threads on the subsutural fold and two riblets below the periphery on the spire whorls. They seem to be a transition to *P. melvilli* Powell, 1969 in sculpture, but that species is almost half the size, with a proportionally higher spire and truncated anterior end. However, the general pattern of sculpture, shell outline and the character of protoconch are similar in all JME shells and those from stn 180 are provisionally assigned to *P. agalma* pending examination of additional material.

DISTRIBUTION. Ceylon and Gulf of Aden, 655–848 m.

Genus *CERITOTURRIS* Dall, 1924

Type species: *Ceritoturris bittium* Dall, 1924 (original designation)

?*Ceritoturris* sp.

Fig. 62

MATERIAL. stn 42, 1 shell.

A single heavily damaged shell ($H = 11.8$ mm) from stn 42 can possibly be referred to *Ceritoturris* on the basis of its resemblance to both type species and *C. nataliae* Kilburn, 1988. The very bad condition of the shell renders more precise identification impossible.

DISTRIBUTION. West Arabian Sea, 1415 m.

Genus *PTYCHOBELA* Thiele, 1925

Type species: *Clavatula crenularis* Lamarck, 1816 (= *Murex nodulosus* Gmelin, 1791) (original designation)

Ptychobela cf. *suturalis* (Gray, 1838)

Figs 79 & 80

Drillia suturalis Gray, 1838, p. 29.

Ptychobela suturalis (Gray) – Kilburn, 1989, p. 190, figs 5–6 (holotype) & 7–8.

TYPE LOCALITY. unknown.

MATERIAL. stn 35, 1 shell; stn 188, 2 shells.

These shells are difficult to determine primarily due to the existence of numerous species of uncertain status which have been described within the genus *Drillia* and, as far as it can be judged from drawings (when present) and rather brief descriptions, are similar to the JME material (e.g. *Drillia incerta* E.A.Smith, 1877, *D. atkinsoni* E.A.Smith, 1877, *D. variabilis* E.A.Smith, 1877, etc.). The question cannot be resolved without comparative examination of type material. Nevertheless, these shells are quite comparable with the holotype of *P. suturalis* illustrated by Kilburn (1989). The latter species is however characterized by usually very short axial folds with strong peripheral nodules (but the folds in the holotype are rather long – see Kilburn, 1989, fig. 6). The smaller of the JME shells (stn 188, $H = 22.7$, $D = 7.6$ mm, Fig. 80) differs also in complete absence of additional spiral threads in the interspaces between main cords. The other shell (stn 188, $H = 22.9$, $H_b = 15.6$ mm, upper spire whorls are broken off and only 3.5 last whorls are intact) also lacks additional threads on upper spire whorls, but they appear on penultimate whorl and become rather strong on the body whorl. The anal sinus is similar in shape to that of *P. suturalis*, but some of the sinus scars indicate that during the shell growth the sinus may be quite different: very deep and narrow, asymmetrical, with the upper edge of the slit almost parallel to the suture. The rather large shell from stn 35 ($H = 31.1$, $D = 11.0$ mm, Fig. 79) is characterized by fairly long axials reaching the lower suture and a peculiar spiral sculpture of ribs with the upper (directed adapically) slope being much steeper than the lower. This produces a somewhat tiled pattern and, when illuminated from the shell apex, the sculpture seems to consist of very wide flattened ribs.

DISTRIBUTION. According to Kilburn (1989), *P. suturalis* is a central West Pacific species (from Taiwan and Singapore to Queensland and Western Australia).

***Ptychobela* cf. *nodulosa* (Gmelin, 1791)**

Fig. 84

Murex nodulosus Gmelin, 1791, p. 3562.

Clavatula crenularis Lamarck, 1816, p. 9, pl. 440, figs 3a,b.

Ptychobela nodulosa (Gmelin) – Kilburn, 1989, p. 187–190, figs 1–2) & 3–4 (neotype).

TYPE LOCALITY. unknown.

MATERIAL. stn 188, 1 shell.

The situation with this species is the same as in the preceding case. The JME shell resembles rather closely the neotype of *P. nodulosa* designated and illustrated by Kilburn (1989) in the shell outline and the character of sculpture. However, it lacks the characteristic colour pattern of *P. nodulosa* being of uniform light-brown colour (the shell was dead collected and probably faded), and has a slightly higher spire ($H_s/H = 0.49$ vs. 0.41 in the neotype of *P. nodulosa*) and more convex whorls. A characteristic feature of the shell considered is that axial folds extend from suture to suture on the uppermost whorls and only on 8th teleoconch whorl the typical subsutural slope without axial sculpture is developed.

Subfamily **TURRINAE** H. & A. Adams, 1953

Genus **GEMMULA** Weinkauff, 1875

Type species: *Pleurotoma gemmata* Reeve, 1843 (subsequent designation Cossmann, 1896) (= *Gemmula hindsiana* Berry, 1958)

***Gemmula* (*Gemmula*) *vagata* (E.A.Smith, 1895)**

Figs 63–65

Pleurotoma vagata E.A.Smith, 1895, p. 3, pl. 1, fig. 3; 1904, p. 456; Alcock *et al.*, 1907, pl. 14, figs 3, 3a.

Gemmula vagata (E.A.Smith) – Powell, 1964, p. 258–259, pl. 196, fig. 10.

TYPE LOCALITY. ‘Investigator’, stn 172, off Trincomalee, Ceylon, 200–350 fms.

MATERIAL. stn 176, 8 shells, stn 188, 3 shells.

The largest shell is 49.8 mm in height (apex slightly broken). Examination of a growth series showed that its characteristic features (i.e. almost vertical sides of whorls, very strongly excavated subsutural fold, and channelled sutures) are developed only when the shell reaches a certain size (approximately 35 mm in height and more than 10 teleoconch whorls). Young shells can be determined only by comparison with larger specimens. A peculiar and previously undescribed feature of the species is the presence of spiral lirae inside the aperture in large individuals.

DISTRIBUTION. Gulf of Aden to Andaman Islands, 338–1061 m.

***Gemmula* (*Gemmula*) *amabilis* (Jickeli in Weinkauff, 1875)**

Figs 66, 67 & 71

Pleurotoma amabilis Jickeli in Weinkauff, 1875, p. 29, pl. 6, figs 4, 6.

Pleurotoma (*Gemmula*) *amabilis* Weinkauff – Sturany, 1903, pl. 3, figs 3a–c.

Gemmula amabilis (Weinkauff) – Powell, 1964, p. 261–262, pl. 200, fig. 1, pl. 201, figs 3–7.

?*Gemmula amabilis* (Weinkauff) – Kosuge, 1990, p. 153–154, pl. 55, fig. 13, text-fig. 6; Kosuge, 1992, p. 163, pl. 58, fig. 1, text-figs 7, 11, 12–14.

TYPE LOCALITY. Massawa (Ethiopia), Red Sea.

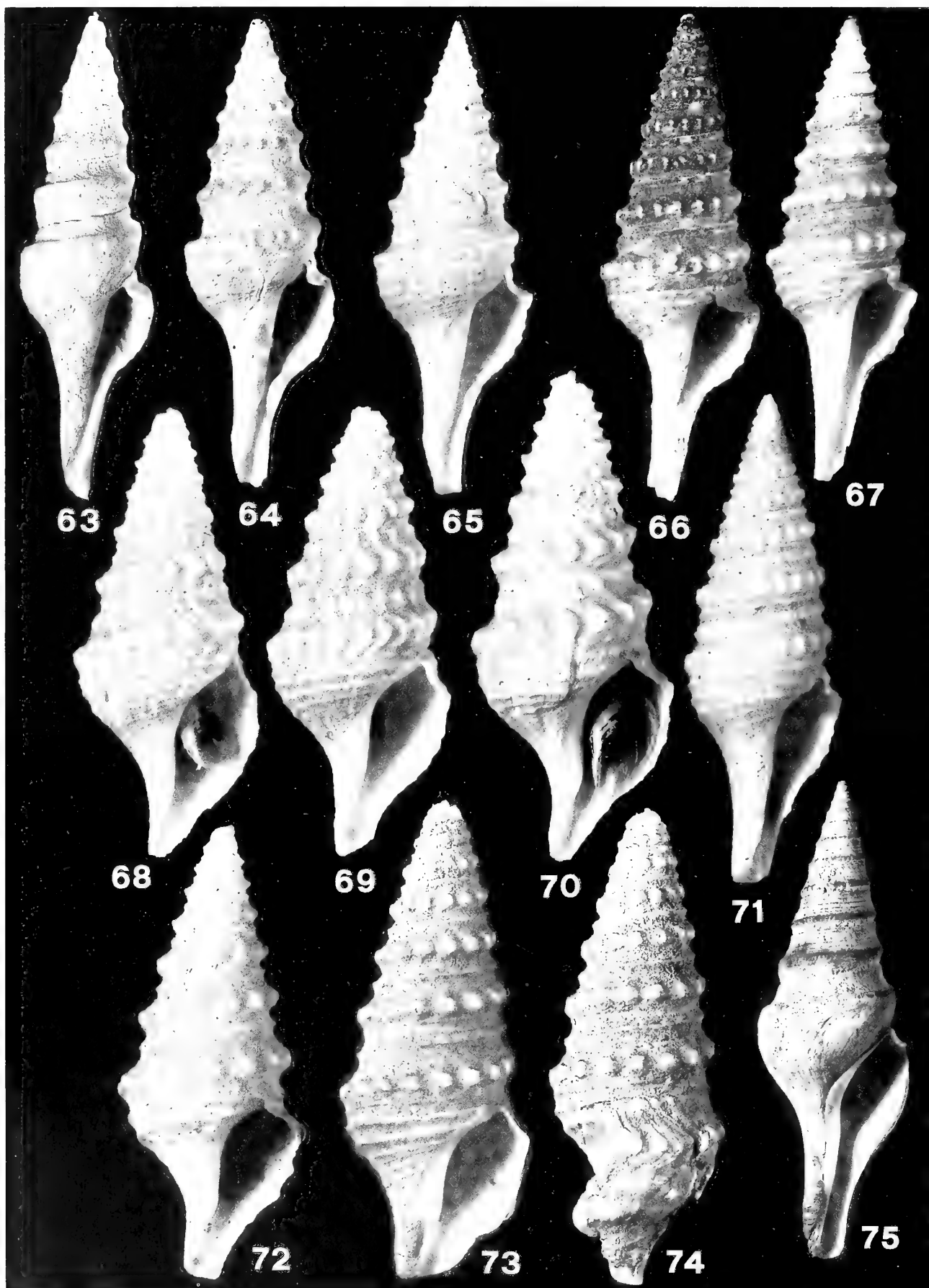
MATERIAL. stn 34, 18 specimens and shells; stn 119, 1 shell; stn 145, 1 specimen and 2 shells; stn 176, 2 shells; stn 185, 1 shell; stn 188, 2 shells; stn 193, 3 specimens.

The taxonomy of this species is rather confused. The name *amabilis* had long been unused until Powell (1964) applied it to shells from the JME material (the specimen from the JME stn 176 figured by him (Powell, 1964, p. 200, fig. 1) was not found). However, Powell expressed some doubts on the identification of JME specimens as *G. amabilis*, having indicated certain differences from the sketchy and rather inadequate original figures.

Kilburn (1983) reported that the types of *Pleurotoma amabilis* were probably lost and therefore the name *amabilis* must remain a *nomen dubium*. He also compared the specimen figured by Powell with *G. pulchella* Shuto, 1961 from the Pliocene of Japan. The latter species is characterized by smaller and much more numerous gemmules (29 on the body whorl of 10.2 mm holotype and up to 34 at the shell height of 26.57 mm – Shuto, 1965).

Later on, Kosuge (1990, 1992) used the name *amabilis* for North-Western Australian shells and at the same time mentioned that Powell's specimen differs from the original drawings and, as far as it can be judged from the text (Kosuge, 1990, p. 154), may not be conspecific with *amabilis*. The shells figured by Kosuge as *G. amabilis*, actually resemble *G. gemmulina* (von Martens, 1902) *sensu* Powell, 1964 more in the shell outlines and the character of spiral sculpture of alternating primary cords and intermediate threads. The latter species is distributed from Taiwan to Indonesia (Powell, 1964), which is far closer to North-Western Australia than the Red Sea and the Gulf of Aden.

Despite the obviously ambiguous status of the name *amabilis*, it seems reasonable to conserve its application to the Gulf of Aden shells similar to those described by Powell, because no other available name for them exists. Perhaps, the examination of a large series of the Red Sea *Gemmula*, especially from the type locality of *amabilis*, would clear up the question of proper application of the name. The specimens of *G. amabilis* are characterized by a small slender shell (up to 25.9 mm, usually 22–25 mm) with more or less channelled sutures, a moderately developed subsutural fold covered by 1–3 riblets, 2–3 prominent and widely spaced cords on the upper shell base without intermediate threads, few (usually two) thin threads on the subsutural slope, and 16–24 peripheral gemmae on the body whorl (usually 22, mean 20.7 at the shell height 18.2–25.9 mm; the number of gemmae does not show a strict correlation with the shell height). This deep-water species, due to its small size, can be confused with young specimens of other species of *Gemmula*. However, the presence of the ‘tertiary’ apertural



notch (characteristic for mature individuals of *Gemmula* – see Kantor & Sysoev, 1991) in one of the shells ($H = 20.2$) indicates that the mentioned shell size characterizes adult specimens of *G. amabilis*.

DISTRIBUTION. North-western Indian Ocean, 494–2000 m; also probably from north-western Australia, 300–496 m.

***Gemmula (Gemmula) cf. congener* (E.A. Smith, 1894)**

Pleurotoma congener E.A. Smith, 1894, p. 160–161, pl. 3, figs 4, 5.
Gemmula congener subspecies *congener* (E.A. Smith) – Powell, 1964, p. 251–252, p. 191, figs 1–4; Cernohorsky, 1987, p. 123–124, figs 1, 2–3 (holotype), 4–5.

TYPE LOCALITY. Bay of Bengal, 128 m.

MATERIAL. stn 176, 1 shell.

A single broken and heavily worn shell ($H = 39.6$ mm) can probably be referred to *G. congener* by its very strong gemmulated subsutural fold.

DISTRIBUTION. Indian Ocean, 198–732 m.

Subgenus *UNEDOGEMMULA* MacNeil, 1960

Type species: *Pleurotoma unedo* Kiener, 1839–40 (original designation)

***Gemmula (Unedogemmula) unedo* (Kiener, 1839–1840)**

Fig. 75

Pleurotoma unedo Kiener, 1839–1840, p. 19, pl. 14, fig. 1.
Gemmula (Unedogemmula) unedo (Kiener) – Powell, 1964, p. 269–270, pl. 175, figs 1, 6, pl. 208, figs 1, 2; Kosuge, 1988, p. 121–122, text-figs 4, 13–15, pl. 47, figs 9, 10.
Pleurotoma invicta Melvill, 1910, p. 15, pl. 2, fig. 27.

TYPE LOCALITY. ‘Mers de l’Inde’ (*unedo*), Persian Gulf (*invicta*).

MATERIAL. stn 145, 1 specimen.

The shell from stn 145 is peculiar in the complete absence of spiral sculpture on the body whorl. The sculpture is represented only by very rough growth lines which is probably a senile abnormality.

DISTRIBUTION. Persian Gulf to Japan, 73–503 m.

Subgenus *PTYCHOSYRINX* Thiele, 1925

Type species: *Pleurotoma (Subulata) bisinuata* von Martens, 1901 (original designation)

***Gemmula (Ptychosyrinx) bisinuata* (von Martens, 1901)**

Figs 72–74

Pleurotoma (Subulata) bisinuata von Martens, 1901, p. 17.
Drillia (Subulata) bisinuata (von Martens) – von Martens, 1903 [1904], p. 82, pl. 1, fig. 8.
Ptychosyrinx bisinuata (von Martens) – Thiele, 1925, p. 176(210), text-fig. 28 (rad.), pl. 46(34), fig. 28 (operc.); Powell, 1964, p. 289–290, pl. 223, figs 1, 2.
Gemmula (Ptychosyrinx) bisinuata (von Martens) – Cernohorsky, 1987, p. 130, figs 15–17.

TYPE LOCALITY. ‘Valdivia’, stn 264, near the coast of Somalia, 1079 m.

MATERIAL. stn 119, 1 specimen and 1 shell; stn 184, 1 specimen.

The species is rather similar to the closely related *G. teschi* (Powell) (see below). The main differences are that, in *G. bisinuata*, the subsutural rib is clear, thin, straight or slightly wavy, without nodules; the sutures are poorly seen and very shallowly impressed. In *G. teschi*, the subsutural rib is very weakly developed or absent (or there is a weak to moderate subsutural fold), covered with nodules which are the continuation of axial folds; the sutures are clear, more or less channelled. Additionally, the spiral ribs on the shell base in *G. bisinuata* are clear and prominent; two lower ribs out of three upper ones are much stronger than the other. In *G. teschi*, the ribs are thinner, more uniform, more numerous and closely spaced; the shell base is evenly convex.

DISTRIBUTION. East Africa from the Gulf of Aden to Malagasy, 818–1463 m.

***Gemmula (Ptychosyrinx) teschi* (Powell, 1964)**

Figs 68–70

Ptychosyrinx timorensis teschi Powell, 1964, p. 291–292, pl. 223, figs 5, 6; Abbott & Dance, 1990, p. 238, fig. (holotype).

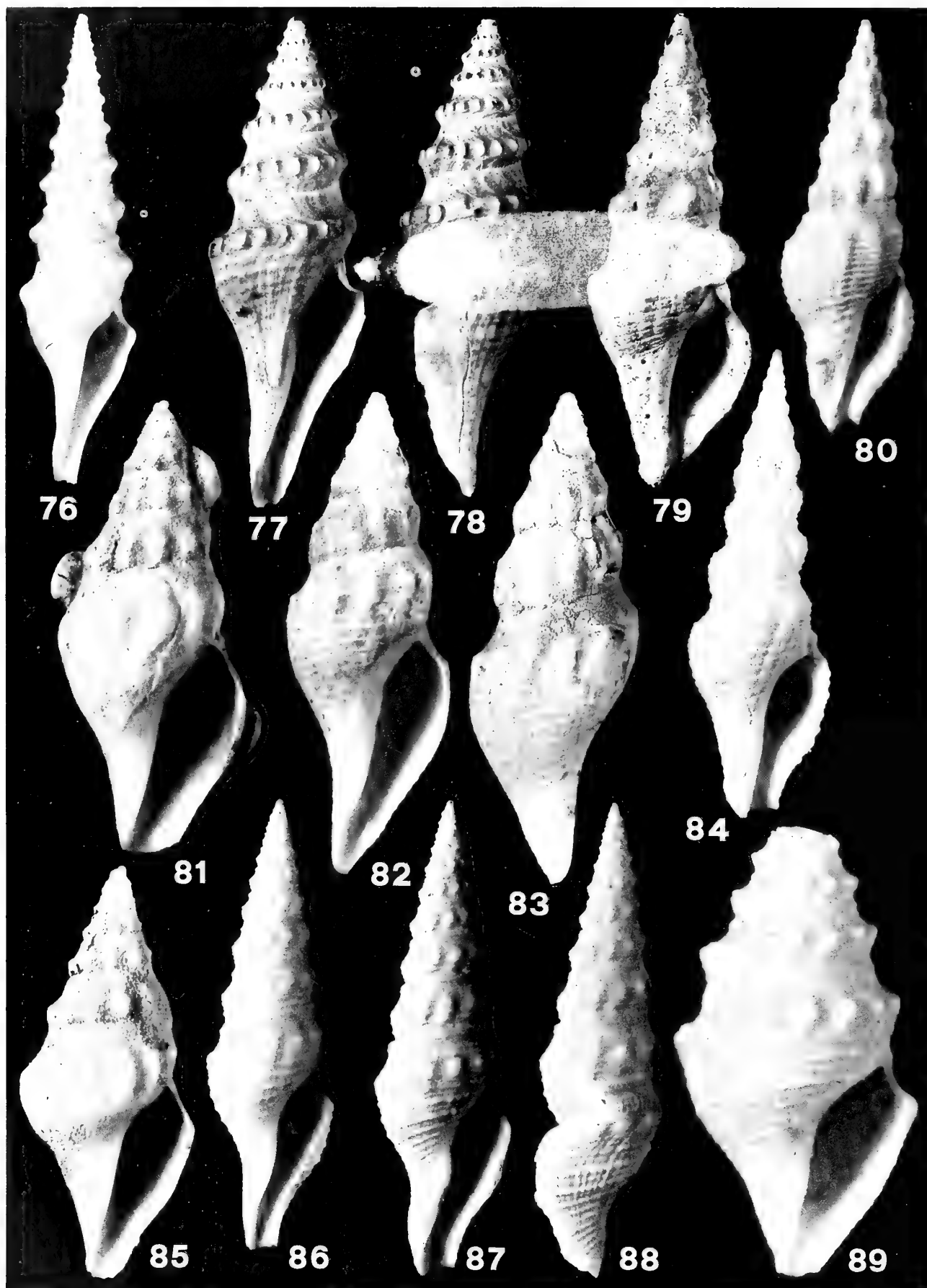
TYPE LOCALITY. ‘Albatross’, stn 5587, NW of Sipadan Id., Borneo, 415 fms.

MATERIAL. stn 118, 6 specimens.

Although having been described as a subspecies, *G. teschi* obviously warrants specific rank from the fossil *G. timorensis* (Tesch, 1915) in having a much broader fusiform shell. The specimens from the JME material vary in the prominence of spiral ribs on the shell base and the number of peripheral tubercles (17–22 on the body whorl, mean 19). In no specimen is the subsutural fold as strong and regularly gemmate as in the holotype.

DISTRIBUTION. Indonesia and Zanzibar, 635–1789 m.

Figs 63–75 *Gemmula* spp. **63–65** – *Gemmula (Gemmula) vagata* (E.A. Smith, 1895), stn 176 (**63**, **64**) and 188 (**65**), $H = 48.9$ (**63**), 33.3 (**64**) and 36.3 (**65**) mm; **66**, **67**, **71** – *G. (G.) amabilis* (Jickeli in Weinkauff, 1875), stn 193 (**66**), 34 (**67**) and 145 (**71**), $H = 25.8$ (**66**), 23.3 (**67**) and 21.3 (**71**) mm; **68–70** – *Gemmula (Ptychosyrinx) teschi* (Powell, 1964), stn 118, $H = 28.2$ (**68**), 27.5 (**69**) and 24.7 (**70**) mm; **72–74** – *G. (P.) bisinuata* (von Martens, 1901), stn 119 (**72**) and 184 (**73**, **74**), $H = 18.8$ (**72**) and 30.5 (**73**, **74**) mm; **75** – *Gemmula (Unedogemmula) unedo* (Kiener, 1839–40), stn 145, $H = 95.5$ mm.



Genus **LUCERAPEX** Iredale, 1936

Type species: *Pleurotoma casearia* Hedley & Petterd, 1906 (original designation)

***Lucerapex adenica* Powell, 1964**

Fig. 76

Lucerapex adenica Powell, 1964, p. 286–287, pl. 221, fig. 3.

TYPE LOCALITY. 'Mabahiss' (John Murray Expedition), stn 34, Gulf of Aden, 1022 m.

MATERIAL. stn 193, 1 shell; also described from stn 34 and 191 by Powell (1964).

The specimen figured (H = 31.0 mm which is slightly more than in the type specimens) was probably omitted by Powell whose original description of the species was based on the JME material.

DISTRIBUTION. Gulf of Aden, 274–1080 m.

***Lucerapex molengraaffi* (Tesch, 1915)**

Figs 77 & 78

Pleurotoma (s.str.) *molengraaffi* Tesch, 1915, p. 28, pl. 77, figs 54–56.

Lucerapex molengraaffi (Tesch) – Powell, 1964, p. 287–288, pl. 220, figs 3, 4, pl. 221, figs 1, 2.

TYPE LOCALITY. Timor, Pliocene.

MATERIAL. stn 145, 1 shell.

DISTRIBUTION. Maldives Islands, Borneo, Celebes, Philippines, 464–1022 m.

Family **CONIDAE** Fleming, 1822

Subfamily **CLATHURELLINAE** H. & A. Adams, 1858

Genus **BORSONIA** Bellardi, 1839

Type species: *Borsonia prima* Bellardi, 1839 (monotypy)

***Borsonia ochracea* Thiele, 1925**

Figs 82 & 83

Borsonia ochracea Thiele, 1925, p. 183–184 (217–218), pl. 38(26), figs 1–3, text fig. 26.

TYPE LOCALITY. 'Valdivia', stn 257, (off Somalia), 1644 m.

MATERIAL. stn 122, 1 specimen; stn 184, 1 shell.

The JME material agrees well with Thiele's original figures differing only in having somewhat narrower and more widely spaced spiral ribs (though this may result from rather schematized appearance of spiral sculpture in many Thiele's figures). The columellar pleat is very weak and can be seen only

if the aperture is broken. The radular teeth are also very similar to those figured by Thiele; the operculum is absent as in the type specimens.

DISTRIBUTION. East Africa from Zanzibar to the Gulf of Aden, 693–1644 m.

Subgenus **CORDIERIA** Rouault, 1848

Type species: *Cordieria iberica* Rouault, 1850 (subsequent designation Cossmann, 1896)

***Borsonia (Cordieria) symbiophora* Sysoev, new species**

Figs 5, 12, 13, 81 & 85

MATERIAL. stn 26, 4 specimens (paratypes No. 1993103); stn 118, 6 specimens (holotype No. 1993101 and 5 paratypes No. 1993102).

DESCRIPTION OF HOLOTYPE. The shell is of medium size for the genus, broadly fusiform, rather stout, strong, white under olivaceous periostracum and light-brown inside the aperture, and consisting of 7 whorls. The protoconch is missing, and the upper whorls are eroded. Definitive whorls are obtusely angled at the periphery, slightly concave at the subsutural slope and weakly convex below. The body whorl is rather large (0.65 of the shell height), the shell base is weakly convex, and passes smoothly into the canal. The sutures are wavy and channelled. The axial sculpture consists of wide, rounded, short folds which are obsolete in the middle part of the subsutural slope (they can be traced as very low tubercles just below the suture) and do not reach the shell base. The folds are most prominent just below the subsutural slope at the whorl periphery. There are 12 folds on the body whorl and 11 on the penultimate. Spiral sculpture is represented by wide, rounded, low ribs separated by narrow grooves and covering the entire shell surface. On the shell base, the ribs become subobsolete, with wider interspaces. The growth lines override the ribs making their surface rugose. The aperture is rather wide and not differentiated from the wide and short canal. The inner lip is smooth, covered by glossy callus. The anal sinus is symmetrical, wide and shallow, its deepest part is situated in the middle of the subsutural slope. H = 27.4, Hb = 17.8, Ha = 13.9, D = 11.5 mm.

The paratypes are very variable in the character of spiral sculpture which may be either well developed or subobsolete to obsolete. There is no correlation between the prominence of spiral ribs on the subsutural slope and on the rest part of the whorl. Paratypes of smaller size have more biconic shells with narrower canals.

The protoconch is broken in almost all specimens. In the only specimen with an intact but eroded protoconch, it seems to consist of 1.5 rapidly increasing whorls.

The radular teeth are typical of borsoniid group of genera, small (0.24 mm in paratype from stn 185, H = 21.8 mm), straight, rather short, with a cusp at the tooth base.

The operculum is small, leaf-shaped, vestigial, with a terminal nucleus. In one paratype from stn 185 the operculum, probably

Figs 76–89 Turrinae, Zonulispirinae and Clathurellinae. **76** – *Lucerapex adenica* Powell, 1964, stn 193, H = 31.0 mm; **77, 78** – *L. molengraaffi* (Tesch, 1915), stn 145, H = 25.1 mm; **79, 80** – *Ptychobela* cf. *suturalis* (Gray, 1838), stn 35 (**79**) and 188 (**80**), H = 31.1 (**79**) and 22.7 (**80**) mm; **81, 85** – *Borsonia (Cordieria) symbiophora* Sysoev, new species, holotype (**81**) and paratype, stn 118, H = 23.8 mm (**85**); **82, 83** – *Borsonia (Borsonia) ochracea* Thiele, 1925, stn 122, H = 37.0 mm; **84** – *Ptychobela* cf. *nodulosa* (Gmelin, 1791), stn 188, H = 29.6 mm; **86–88** – *Typhlomangelia maldivica* Sysoev, new species, holotype (**86**) and paratype, stn 143, H = 32.0 mm (**87, 88**); **89** – *T. adenica* Sysoev, new species, holotype.

as a result of damage and subsequent repair, is very small, subquadrate, with central nucleus (Fig. 12).

All specimens of *B. symbiophora* bear actinians on their shells and are often entirely covered with them.

The new species differs from all known Recent species of *Borsonia*, in its stout shell with typically uniform spiral sculpture and smooth columella.

The species is quite comparable with species of *Borsonia* and, especially of the *Cordieria* subgenus primarily differing in the absence of columellar plicae and the presence of operculum. However, the prominence (and even presence) of columellar plicae can vary greatly among species of the same genus and sometimes among shells of the same species. The presence of an operculum also cannot be considered as a diagnostic character because it is very patchily distributed in the subfamily, where repeated and independent reduction and loss of operculum undoubtedly occurred, and many faunas demonstrate a full range of species with well developed, vestigial or missing operculum (e.g. Eastern Pacific – see McLean, 1971).

B. symbiophora is also similar to species of the subgenus *Borsonellopsis* McLean, 1971 of the genus *Borsonella* Dall, 1890. The type species of *Borsonellopsis*, *Leucosyrinx erosina* Dall, 1908, possesses similar sculpture and shell outlines as well as a vestigial operculum, and lacks columellar plicae. On the other hand, it differs considerably from *Borsonella* s.str. and may not be congeneric.

DISTRIBUTION. Gulf of Aden and off Mombasa (Kenya), 1789–2312 m.

Genus *BATHYTOMA* Harris & Burrows, 1891

Type species: *Murex cataphractus* Brocchi, 1814 (monotypy)

Subgenus *PARABATHYTOMA* Shuto, 1961

Type species: *Pleurotoma striatotuberculata* Yokoyama, 1928 (original designation)

The differences between the generally accepted subgenera of *Bathytoma* (see Powell, 1966) seem to be rather slight. Kilburn (1986) mentioned that *Parabathytoma* differs from *Micantapex* in having radular teeth without an elongate base and in the absence of brephic arcuate riblets at the place of the protoconch transition into teleoconch whorls. However, in all the species described below, the presence of long, curved teeth without an elongate base is associated with the presence of arcuate riblets at the place of the protoconch termination, i.e. these species possess characters of both *Parabathytoma* and *Micantapex* sensu Kilburn. Thus, the only feature distinguishing these subgenera is the shape of radular teeth. The question is further complicated by the fact that the type species of *Parabathytoma* is a fossil *Pleurotoma striatotuberculata* Yokoyama, 1928, while the radula of type species of *Micantapex*, *Bathytoma agnata* Hedley & Petterd, 1906, is unknown. Nevertheless, the species listed below are provisionally included into *Parabathytoma* on the basis of their radular morphology.

Bathytoma (Parabathytoma) prodicia Kilburn, 1986

Figs 90 & 91

Bathytoma (Parabathytoma) regnans (non Melvill, 1918) – Kilburn, 1971, p. 31, figs 2c, 2f, 4b.

Bathytoma (Parabathytoma) prodicia Kilburn, 1986, p. 643, figs 22–23.

TYPE LOCALITY. East of Bazaruto Island (Southern Mozambique), 300–310 fms.

MATERIAL. stn 119, 1 shell.

The shell from the JME material differs from the holotype figured by Kilburn in having less prominent peripheral nodules, shallower anal sinus, and flattened shell base. However, all other essential conchological characters including the shell proportions ($D/H = 0.43$, $Ha/H = 0.52$) are similar to *B. prodicia*. An additional smaller ($H = 23.5$ mm) specimen collected off Zanzibar by R/V 'Vityaz' (stn 4680, 740 m) is in some respects intermediate between the typical *B. prodicia* and the JME shell.

DISTRIBUTION. Southern Mozambique to Zanzibar, 420–1463 m.

Bathytoma (Parabathytoma) oldhami (E.A. Smith, 1899)

Figs 7 & 92–93

Pleurotoma (Bathytoma) oldhami E.A. Smith, 1899, p. 238.

Pleurotoma oldhami E.A. Smith – Alcock & McArdle, 1901, pl. 9, figs 2, 2a.

TYPE LOCALITY. 'Investigator', stn 229, off Travancore coast, 360 fms.

MATERIAL. stn 145, 1 specimen.

The JME specimen is of approximately the same size as the holotype and very similar to the figure of the latter, differing only in slightly broader shell ($H = 41.0$ mm, $D = 15.8$ mm vs. 43 and 15 mm in the holotype). The protoconch consists of about 1.5 smooth globose whorls followed by several arcuate axial riblets which gradually become stronger and pass into the teleoconch sculpture. The radular teeth (Fig. 7) are long and strongly curved, of typical shape for the subgenus. The mean tooth length is 0.77 mm.

DISTRIBUTION. Southern India and Maldives Islands, 494–658 m.

Bathytoma (Parabathytoma) regnans Melvill, 1918

Figs 8, 16 & 94–97

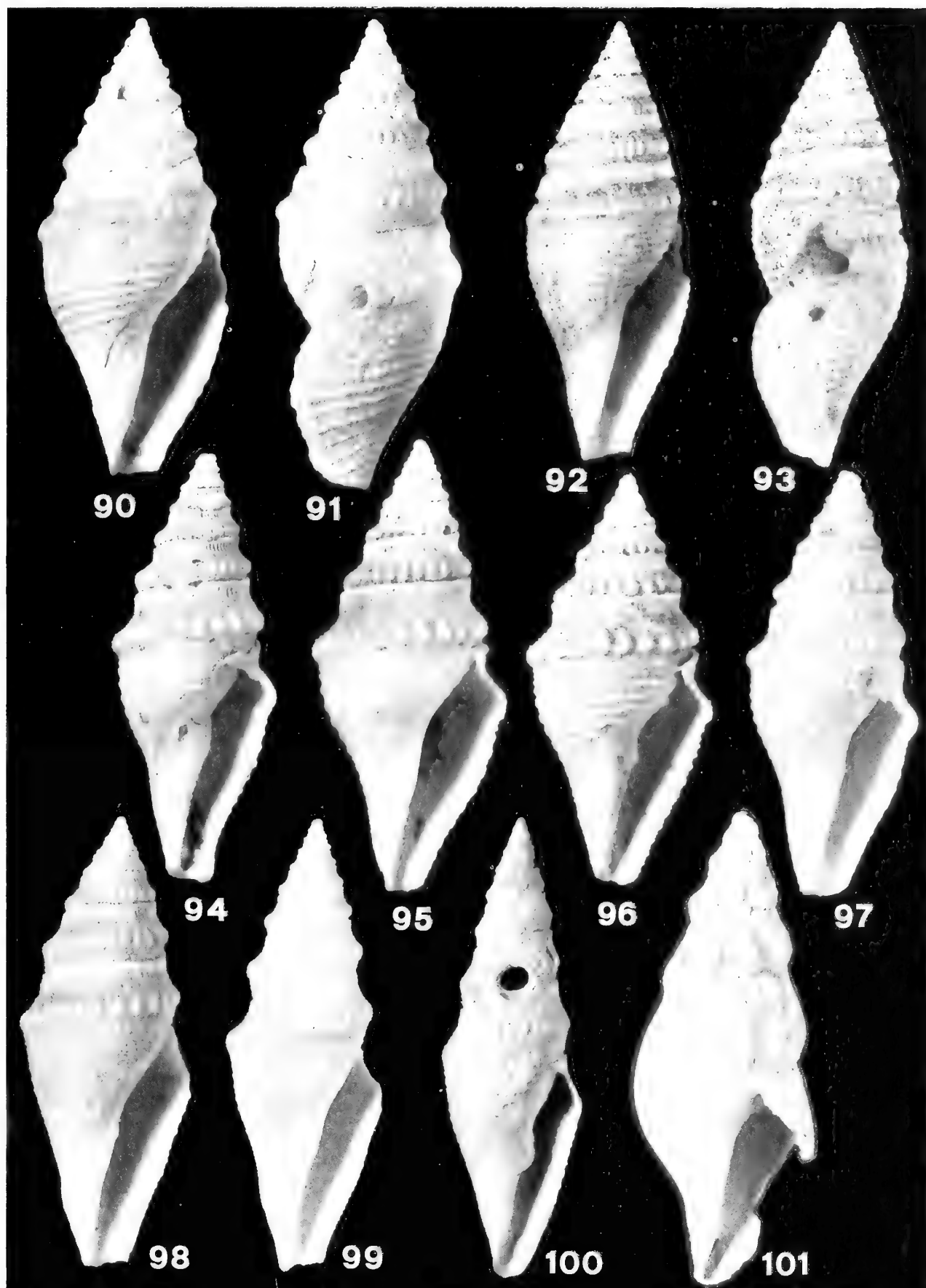
Bathytoma regnans Melvill, 1918, p. 68, textfig.

Bathytoma regnans Melvill – Kilburn, 1986, p. 718, fig. 168 (holotype).

TYPE LOCALITY. Indian Ocean, Investigator Expedition (probably the Bay of Bengal).

MATERIAL. stn 34, 1 specimen and 5 shells; stn 188, 2 shells; stn 193, 6 shells.

Figs 90–101 Clathurellinae. **90, 91** – *Bathytoma (Parabathytoma) prodicia* Kilburn, 1986, stn 119, $H = 32.3$ mm; **92, 93** – *B. (P.) oldhami* (E.A. Smith, 1899), stn 145, $H = 41.0$ mm; **94–97** – *B. (P.) regnans* Melvill, 1918, stn 188 (**94, 97**), 34 (**95**) and 193 (**96**), $H = 27.5$ (**94**), 26.6 (**95**), 24.4 (**96**) and 25.5 (**97**) mm; **98–100** – *B. (P.) fissa* (von Martens, 1901), stn 176, $H = 35.3$ (**98**), 34.7 (**99**) and 38.4 (**100**) mm; **101** – *Typhlosyrinx praecipua* (E.A. Smith, 1899), stn 184, $H = 30.2$ mm.



The species is rather variable in the shell proportions: the shell may be elongated (Fig. 94) and very similar to the holotype figured by Kilburn (1986), or more stout and broad (Figs 95 & 96). The H/D ratio varies from 2.03 to 2.55 (2.44 in the holotype). The prominence of the columellar pleat can also vary up to almost complete absence. However, there are rather constant features which are characteristic of the species and distinguish it from *B. fissa* (see below). These are a strongly projecting peripheral keel, distant primary spiral cords with a thin secondary rib in most interspaces, and low position of the peripheral keel, which is bordered or almost bordered by a deeply channelled suture even on the last spire whorls. The protoconch is similar to that of *B. oldhami*. Radular teeth are typical for the subgenus, awl-shaped, curved, and rather short. The mean tooth length is 0.46 mm at H = 26.6 mm. The operculum is small, oval, with subterminal nucleus.

DISTRIBUTION. Gulf of Aden and, probably, the Bay of Bengal, 528–1080 m.

***Bathytoma (Parabathytoma) fissa* (von Martens, 1901)**

Figs 9, 17 & 98–100

Pleurotoma (Dolichotoma) fissa von Martens, 1901, p. 18.

Genota (Dolichotoma) fissa – von Martens, 1903 [1904], p. 87, pl. 1, fig. 14.

TYPE LOCALITY. ‘Valdivia’, stn 264 (Somalia), 1079 m.

MATERIAL. stn 176, 2 specimens and 12 shells.

The species differs from *B. regnans* in having closely set spiral cords, with almost equally strong granular secondary cords in the interspaces, and less prominent peripheral keel which is situated rather high on last spire whorls. The sutures are less distinctly channelled than in *B. regnans*. The shell proportions and the prominence of peripheral keel may vary (Figs 98–100). There are one to three more or less developed columellar pleats; usually two pleats are present and the upper one may be subdivided into two by a groove. The radula and operculum are similar to those of *B. regnans*. The mean tooth length is 0.51 mm at H = 35.3 mm.

Shells from an additional sample (R/V ‘Akademik Mstislav Keldysh’, stn 1089, Tajoura Rift, Gulf of Aden, 857–900 m) show the same characteristic features and the same range of variability but are of larger size (up to 42.5 mm in height) and possess 1 (usually) or 2 columellar pleats.

DISTRIBUTION. Somalia and Gulf of Aden, 665–1079 m.

Genus **TYPHLOMANGELIA** G.O.Sars, 1878

Type species: *Pleurotoma nivale* Loven, 1846 (monotypy)

***Typhlomangelia adenica* Sysoev, new species**

Figs 4, 14 & 89

MATERIAL. stn 26, 1 shell (paratype No. 1993106); stn 185, 2 specimens (holotype No. 1993104 and paratype No. 1993105).

DESCRIPTION OF HOLOTYPE. The shell is small, broad, turreted, solid, covered by thin light-brown periostracum, and consists of 4 remaining whorls. Protoconch and probably some upper whorls are missing. The whorls are strongly angled at the periphery, the subsutural slope is concave. There is a weak

subsutural fold. Sutures are very shallow and indistinct. The body whorl is large, and the shell base is weakly convex and not differentiated from the canal. The axial sculpture consists of numerous narrow oblique folds reaching the lower suture and abruptly disappearing on the subsutural slope. The folds form pointed tubercles just below the subsutural slope. On the body whorl, they rapidly weaken downwards and do not reach the shell base. There are 19 folds on the body whorl and 15 on the penultimate. The subsutural slope is smooth except for growth lines. A single spiral cord is situated on the subsutural fold, 2–4 cords are present below the subsutural slope on the spire whorls, and there are about 15 low, widely and evenly spaced cords on the body whorl, which become weaker towards the anterior end and finally disappear. The aperture is oval, not differentiated from the straight and short canal. The inner lip is covered with a white callus which is thickened and becomes distinctly bordered on the canal. The anal sinus is deep, broad and rounded, slightly asymmetrical, its deepest point is situated just below the middle of subsutural slope. H = 10.2, Hb = 6.6, Ha = 4.7, D = 5.6 mm.

The paratypes are very similar to the holotype but smaller (H = 7.7, D = 4.5 in paratype from stn 185 and H = 6.9, D = 4.1 in paratype from stn 26). The operculum is rather large in comparison to the aperture size, broadly leaf-shaped, with a terminal nucleus. Radular teeth are typical of the genus, awl-shaped, with short and straight shaft and relatively broad base, 0.2 mm in length.

The species differs from all other species of the genus in its very small, broad shell, with a very short and straight canal.

DISTRIBUTION. Gulf of Aden, 2000–2312 m.

***Typhlomangelia maldivica* Sysoev, new species**

Figs 6, 15 & 86–88

MATERIAL. stn 143, 7 specimens (holotype No. 1993107 and 6 paratypes No. 1993108).

DESCRIPTION OF HOLOTYPE. The shell is elongate fusiform, slender, with a high spire, rather solid, covered with thin grayish-brown periostracum, and consists of protoconch and 9 teleoconch whorls. The protoconch consists of about two globose smooth whorls, the surface is partly eroded. Definitive whorls are angled at the periphery, concave on the subsutural slope, with distinct subsutural fold. The body whorl occupies 0.58 of the shell height, the shell base is weakly convex and passes smoothly into the slightly twisted canal. The sutures are distinctly channelled, especially in last whorls. The axial sculpture consists of rounded folds below the subsutural slope; they are most prominent and tuberculate in their uppermost parts and weaken towards the lower suture. The folds tend to become smoother on last spire whorls, and on the body whorl they are very low and restricted to the whorl periphery. There are 13 folds on the body whorl and 12 on the penultimate. Spiral sculpture is represented by rather strong and widely spaced cords. One (or two on last whorls) strong cord is situated on the subsutural slope, 1–3 cords are developed below the subsutural slope of spire whorls (1 on initial whorls and 3 on the last one), and about 20 cords cover the body whorl and the canal. On the body whorl periphery, a weaker cord is situated in each interspace between primary cords. The subsutural slope of the initial whorls is smooth, but on subsequent whorls 1–5 thin riblets are developed, with a stronger one in the centre of the slope. The aperture is rather narrow, oval. The canal is moderately long. The anal sinus is deep, rounded, slightly

asymmetrical, with the apex situated just below the middle of the subsutural slope. $H = 30.2$, $H_b = 17.4$, $H_a = 13.9$, $D = 8.8$ mm.

The paratypes vary in details of spiral sculpture, especially on the subsutural slope, where several rather strong and evenly spaced riblets may be developed. In some paratypes the spiral cords are more numerous, closely spaced on the canal and more or less irregularly distributed over the body whorl surface. There may be from 13 to 15 axial folds on the body whorl. The largest paratype has $H = 32.0$ and $D = 9.1$ mm.

Operculum is small, oval, with terminal nucleus. Radular teeth are long and narrow, more or less curved, without a solid base, rather large (0.74 mm on the average at $H = 27.8$ mm).

The new species resembles the type species of *Typhlomangelia*, *Pleurotoma nivale* Loven, 1846, differing well in the elongate shell with a high spire and prominent spiral ribs.

DISTRIBUTION. Maldiv Islands, 797 m.

Genus *TYPHLOSyrinx* Thiele, 1925

Type species: *Pleurotoma (Leucosyrinx) vepallida* von Martens, 1902 (original designation)

***Typhlosyrinx praecipua* (E.A.Smith, 1899)**

Fig. 101

Pleurotoma (Surcula) praecipua E.A.Smith, 1899, p. 239; Annandale & Stewart, 1910, pl. 21, figs 4, 4a.

Typhlosyrinx praecipua (E.A.Smith) – Powell, 1969, p. 360–361, pl. 272, figs 2, 3.

TYPE LOCALITY. 'Investigator', stn 229, off Travancore coast (India), 360 fms.

MATERIAL. stn 184, 1 shell.

The shell from stn 184 ($H = 30.2$ mm) corresponds quite well with the description and illustration of the type specimen. Axial folds (11 on the penultimate whorl) abruptly disappear on the border between the penultimate and body whorls. The spiral sculpture is developed only on the whorl periphery and the shell base, and consists of low, broad, flattened, wavy riblets unequal in width and separated by narrow grooves.

DISTRIBUTION. India and Gulf of Aden, 658–1270 m.

Genus *GLYPHOSTOMA* Gabb, 1872

Type species: *Glyphostoma dentiferum* Gabb, 1872 (monotypy)

***Glyphostoma maldivica* Sysoev, new species**

Figs 102 & 103

MATERIAL. stn 145, 1 shell (holotype No. 1993109).

DESCRIPTION. The shell is rather small, thick, solid, yellowish-white, and consists of the protoconch and 5 3/4 teleoconch whorls. The protoconch consists of 3 whorls; its initial part is represented by 1.5 rapidly increasing semi-transparent, smooth whorls followed by more solid angled whorls sculptured below the periphery by a narrow keel. The teleoconch whorls are concave below the suture and angled at the periphery. The sutures are clear, shallow, and wavy. The shell base is weakly convex and passes smoothly into the canal. The

shell surface is distinctly and minutely granular, the granulation is better seen in the interspaces between the axial folds. The growth lines are mostly indistinct. The axial sculpture is represented by rounded folds extending from the subsutural slope to lower suture and, on the body whorl, to the canal. There are 24 such folds on the body whorl and 19 on the penultimate. On the subsutural slope, the axial sculpture consists of numerous curved and rather weak folds with sharpened crests. They generally represent the continuation of main axial folds but there may also be interstitial folds; as a result, the subsutural slope of the body whorl is covered with 32 folds. The spiral sculpture is represented by strong ribs almost equal in prominence to the axial folds. At the intersection with axial sculpture, the ribs form rounded tubercles. The interspaces between spiral ribs are covered by closely set threads. The ribs on the subsutural slope are much smaller corresponding to much smaller axial folds. The aperture is elongate-oval. The inner lip bears two rather prominent pointed tubercles in its middle part and several smaller ones in the lower part. The outer lip is sharply and wavy edged and bordered by a heavy curved varix. The inner surface of the aperture bears one strong tubercle in the upper part and a group of 5 tubercles below. The anal sinus is deep, U-shaped, bordered with callus and constricted at its entrance by a heavy tuberculated callus pad. The canal is straight along most its length and slightly curved backwards near the end. $H = 17.6$, $H_b = 11.8$, $H_a = 9.8$, $D = 8.6$ mm.

In general outline the new species is most similar to *Clathurella perlissa* E.A.Smith, 1904 from the Andaman Islands but differs in the character of sculpture and apertural armament. The species corresponds well to the genus *Glyphostoma* in all important conchological characters such as characteristic protoconch, granular surface, prominent subsutural slope with different sculpture (in contrast to *Etrema*), and strong intersecting spiral and axial ribs.

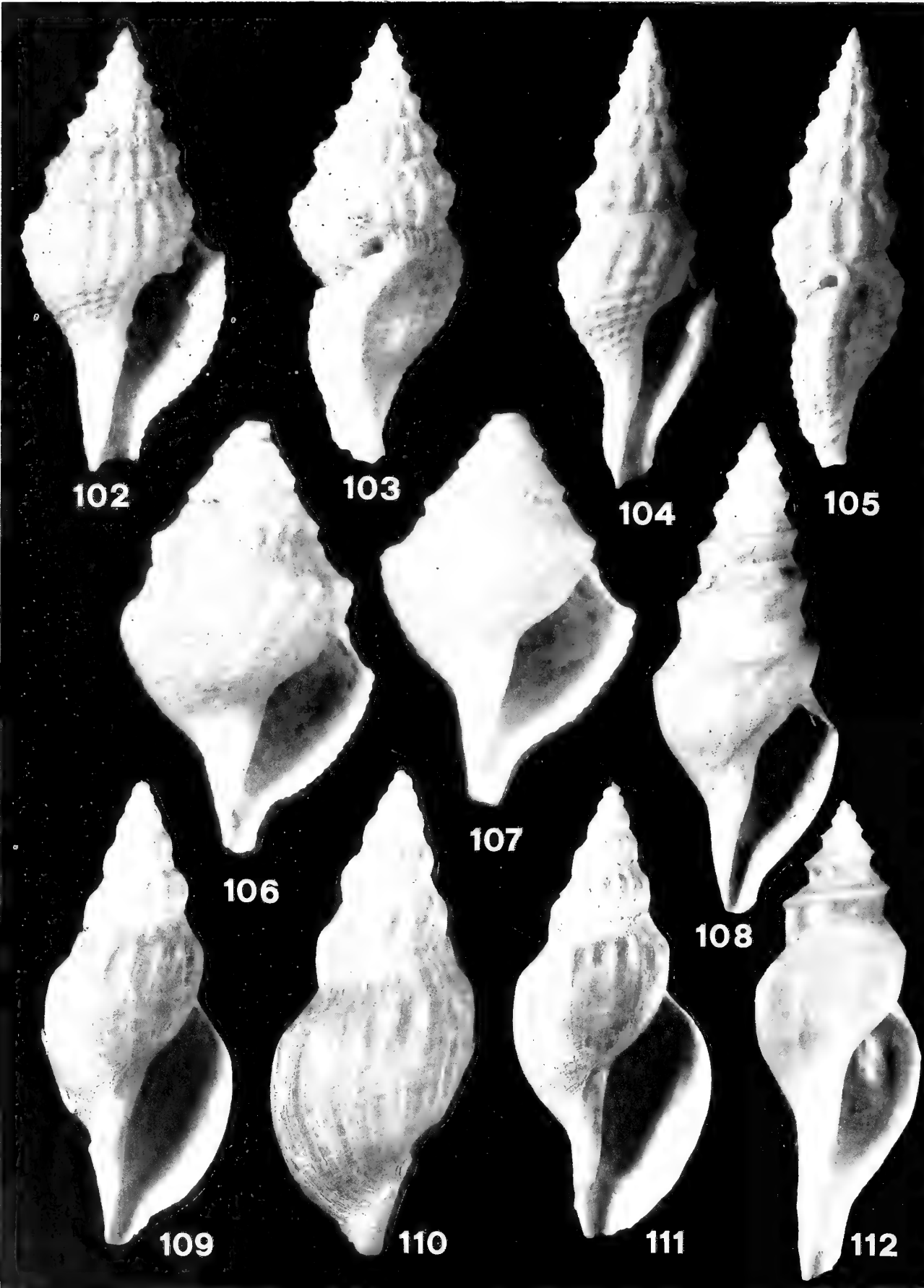
DISTRIBUTION. Maldiv Islands, 494 m.

***Glyphostoma supraplicata* Sysoev, new species**

Figs 104 & 105

MATERIAL. stn 176, 6 shells (holotype No. 1993110 and 5 paratypes No. 1993111).

DESCRIPTION OF HOLOTYPE. The shell is rather small, slender, fusiform, relatively solid, white, consists of protoconch and almost 7 teleoconch whorls. The protoconch consists of 3.5 whorls, the tip is small and papillate. Initial embryonal whorls are smooth, the two last whorls angled, with a cord-like peripheral keel, the second weaker keel encircles the lower suture. The spire is tall, occupies about 0.4 of the shell height. Definitive whorls are angled at the shoulder and in the lower part, the subsutural slope is weakly concave or almost flat. The sutures are clear, shallow, slightly wavy. The entire shell surface is densely and minutely granulated, but the granulation more or less disappears on prominent parts of the sculpture. Growth lines are thin and irregularly elevated. Axial sculpture consists of strong, oblique, rounded folds separated by interspaces approximately equal in width to the folds. The folds reach the canal, gradually weakening on the shell base. On the subsutural slope, they are much weaker, narrower, almost obsolete near the upper suture, and curved in correspondence to the anal sinus scars. There are 15 folds on the body whorl and 13 on the penultimate. Spiral sculpture is represented by broad cords



below the shoulder (2 on the spire whorls and 18 on the body whorl plus canal). The cords are separated by 2–3 times wider intervals. They are often subobsolete in interstices between axial folds but very strong when overridden the latter. On the body whorl, the cords gradually diminish in width and prominence towards the canal end. There are 1–4 (usually 2) thin threads in the interspaces between cords, except between those on the canal, and 3–4 low rounded threads on the subsutural slope. Strong rounded tubercles are formed at the intersection between axial folds and spiral cords resulting in a beaded appearance of the spiral sculpture. The aperture is rather narrow, gradually narrowing towards the canal. The inner lip bears about 13 weak transverse plicae in its lower part, the plicae become closer to each other towards the canal end. There is a moderately developed parietal callus pad which is weakly tuberculate in its lower part. The outer lip has a sharpened edge, with a strong varix behind. Inside the aperture, there are 5 transverse plicae most prominent in the region corresponding to the varix, and a strong tubercle just below the anal sinus. The sinus is semi-tubular, U-shaped, broad and rounded, directed outside in relation to subsutural slope. The canal is long, slightly twisted, and obliquely truncated at the end. $H = 22.6$, $H_b = 13.4$, $H_a = 11.3$, $D = 7.9$ mm.

Paratypes vary in minor details of sculpture, e.g. in the prominence of axials on the subsutural slope, and in more or less strong nodules at the intersections between spiral and axial elements. The largest paratype is 22.6 mm high (protoconch missing).

The new species is quite similar to *G. sultana* (Thiele, 1925) from East Africa, differing in the more slender shell (H/D ratio is 2.70–2.91 vs. 2.55 in the holotype of *G. sultana*) and in the presence of weakened but distinct axial folds on the subsutural slope. A peculiar feature of the new species is the presence of a second keel encircling the suture on last protoconch whorls.

DISTRIBUTION. Gulf of Aden, 655–732 m.

Subfamily DAPHNELLINAE Deshayes, 1863

Genus *CRYPTODAPHNE* Powell, 1942

Type species: *Cryptodaphne pseudodrillia* Powell, 1942 (original designation)

Cryptodaphne gradata (Schepman, 1913)

Fig. 108

Pleurotomella gradata Schepman, 1913, p. 445, pl. 30, fig. 2.

Cryptodaphne gradata (Schepman) – Shuto, 1971, p. 11, pl. 2, figs 4–6.

TYPE LOCALITY. 'Siboga', stn 159, Halmahera Sea, 411 m.

MATERIAL. stn 176, 1 shell.

The shell from the JME material basically conforms to the description and illustrations of the holotype given by Schepman and Shuto (see synonymy). However it differs from the latter in some remarkable characters. The shell is much larger than that in

the holotype (18.5 mm vs. 10.0 mm), with a proportionally higher spire, at approximately the same number of teleoconch volutions (6+ vs. 6). The anal sinus is deeper, with its apex situated lower on the subsutural slope. The initial three whorls of the teleoconch bear oblique axial folds below the peripheral angulation. These folds form nodes on the angulation, making it crenulated, and rapidly weaken towards the lower suture. On subsequent whorls, they become less developed and disappear on the body whorl. The spiral sculpture lacks a regular alternation of strong and weak spirals mentioned by Shuto. The sculpture has a cancellated appearance due to the intersection with growth lines. Also there are widely spaced, thin, and weak but distinct spiral threads on the subsutural slope which were not described by either Schepman or Shuto.

Nevertheless, these differences are not essential and seemingly do not extend beyond the range of intraspecific and geographical variability of *C. gradata*.

DISTRIBUTION. Halmahera Sea and Gulf of Aden, 411–732 m.

Genus *FAMELICA* Bouchet & Warén, 1980

Type species: *Pleurotomella catharinae* Verrill & Smith, 1884 (original designation)

Famelica tajourensis Sysoev & Kantor, 1987

Fig. 112

Famelica tajourensis Sysoev & Kantor, 1987, p. 1257, fig. g, d, e, zh.

TYPE LOCALITY. 'Akademik Kurchatov', stn 1095, Tajoura Rift, Gulf of Aden, 1330–1406 m.

MATERIAL. stn 188, 1 shell.

The JME shell agrees well with the type material and differs mainly in having thin and transparent shell walls compared with rather thick and solid in the type specimens.

The species is rather different from the type species of the genus *Famelica*, but very similar to *F. monotropis* (Dautzenberg & Fischer, 1896), which was included into *Famelica* by the authors of the genus (Bouchet & Warén, 1980). On the other hand, the genus seems to be rather heterogeneous in respect to species originally included into it. Nevertheless, I do not know any other genus which can accommodate *F. tajourensis*. A similar genus is *Pagodidaphne* Shuto, 1983, but it differs in having a less distinct keel on the whorl shoulder and much less elongate body whorl with a short canal.

DISTRIBUTION. Gulf of Aden, 528–1406 m.

Genus *GYMNOBELA* Verrill, 1884

Type species: *Gymnobela engonia* Verrill, 1884 (subsequent designation Cossmann, 1896)

Figs 102–112 Clathurellinae and Daphnellinae. **102, 103** – *Glyphostoma maldivica* Sysoev, new species, holotype; **104, 105** – *G. supraplicata* Sysoev, new species, holotype; **106, 107** – *Gymnobela adenica* Sysoev, new species, holotype (**106**) and paratype, stn 185, $H = 7.1$ mm (**107**); **108** – *Cryptodaphne gradata* (Schepman, 1913), stn 178, $H = 18.5$ mm; **109–111** – *Gymnobela africana* Sysoev, new species, holotype (**109, 110**) and paratype, stn 118, $H = 68.0$ mm (**111**); **112** – *Famelica tajourensis* Sysoev & Kantor, 1987, stn 188, $H = 10.6$ mm.

Gymnobela adenica Sysoev, new species

Figs 106 & 107

MATERIAL. stn 185, 2 specimens (holotype No. 1993112 and paratype No. 1993113).

DESCRIPTION OF HOLOTYPE. The shell is small, broadly biconic, thin, yellowish-white, and consisting of 5 remaining whorls. The protoconch is missing, and the upper teleoconch whorls are eroded. The whorls are angled below the periphery. The subsutural slope is almost flat on the upper spire whorls and concave on the body whorl. The uppermost part of subsutural slope is slightly raised forming an indistinct subsutural fold. The sutures are shallow. Growth lines are mostly indistinct, some of them form clear, narrow, oblique folds regularly set on the upper third of the subsutural fold and approximately twice as numerous as main axial folds. The latter are strongly oblique, narrow, with sharpened crests, and tuberculate at the place of whorl angulation. The folds are separated by narrow intervals, abruptly disappear on the subsutural slope and extend to the lower suture on the spire whorls and to the upper part of the shell base. There are 21 folds on the body whorl and 20 on the penultimate. Spiral ribs (about 30 on the body whorl plus canal) are strong, flattened and uniform except for narrower ones on the canal. Intervals between the ribs are approximately equal to ribs in width. The subsutural slope is densely covered with thin, low, rounded and closely set riblets (about 14 on each of two last whorls). The shell base with a distinct bend passes into a short and straight canal. The aperture is rather small, subrectangular, with the inner lip distinctly bent. The canal is narrow, attenuated at its end. The anal sinus is moderately deep, broadly rounded, its deepest point is situated in the middle of subsutural slope. $H = 9.5$, $H_b = 6.9$, $H_a = 5.1$, $D = 6.0$ mm.

The paratype is very similar to the holotype except for smaller size ($H = 7.1$, $D = 5.3$ mm, 3 teleoconch whorls), smaller H/D ratio, and longer folds formed by growth lines which often occupy the whole subsutural slope. There are 24 main axial folds on the body whorl. The last protoconch whorl preserved is covered with typical diagonally cancellated sculpture.

The species differs from other species of the genus in its small broadly biconic shell with numerous strongly oblique axials and short attenuated canal.

DISTRIBUTION. Gulf of Aden, 2000 m.

Subgenus *BATHYBELA* Kobelt, 1905

Type species: *Thesbia nudator* Locard, 1897 (subsequent designation Dall, 1918)

Gymnobela (Bathybela) africana Sysoev, new species

Figs 109–111

MATERIAL. stn 118, 1 specimen (holotype, No. 1993114) and 1 shell (No. 1993115).

DESCRIPTION OF HOLOTYPE. The shell is large, broadly fusiform, thin but solid, reddish-brown to light-brown, and with a slightly glossy surface. It consists of 6 whorls, the protoconch is missing. The whorls are obtusely angled above the periphery, moderately convex below the angulation and slightly concave above it. The sutures are rather shallowly impressed, clear, straight or wavy in some places. The body whorl is large,

occupies about 0.7 of the shell height; the shell base is weakly convex, with a distinct bend passes into the straight canal. The axial sculpture consists of narrow oblique folds, often with sharpened crests. The folds begin in the lower part of the subsutural slope and extend to the lower suture on the spire whorls and only to the periphery on the body whorl. They are most prominent in the place of the whorl angulation. There are 17 folds on the body whorl and 15 on the penultimate one. The growth lines are indistinct on the whorl surface except the subsutural slope, some of them are thickened and raised. The thickened growth lines, however, do not form the regularly arranged plicae on the subsutural slope which are characteristic of many deep-sea Daphnellinae. The spiral sculpture is represented by rather wide, flattened, wavy ribs unequal in size and separated by narrow grooves. The subsutural slope is smooth except for several very feeble spiral lines. The aperture is broad, the inner lip forms a distinct bend, and the columella is twisted. The anal sinus, judging from the growth lines, is shallow and broad, its deepest point is situated immediately above the middle of subsutural slope. The dried soft body has no operculum.

$H = 54.7$, $H_b = 38.5$, $H_a = 30.1$, $D = 22.7$ mm.

The shell of the paratype is larger than in the holotype ($H = 68.0$, $H_b = 48.2$, $H_a = 38.5$, $D = 30.0$ mm). It was dead-collected and the surface is rather worn. The paratype differs from the holotype mainly in its shorter axial folds developed on the body whorl only at the place of angulation and obsolete in the last quarter of body whorl, and in the canal curved backwards.

The new species is rather similar to *Spergo sibogae* Schepman, 1913 from Indonesia differing in much broader shell ($H/D = 3.0$ in *S. sibogae* and 2.3–2.4 in *G. africana*). It also shows some similarity to *Pontiothauma pacei* E.A. Smith, 1906 from India and Ceylon differing in somewhat more slender shell with short axial folds and faint spiral sculpture.

DISTRIBUTION. East Africa eastward of Mombasa, 1789 m.

Subgenus *THETA* Clarke, 1959

Type species: *Pleurotomella (Theta) lyronuclea* Clarke, 1959 (original designation)

Gymnobela (Theta) daphnelloides (Dall, 1895)

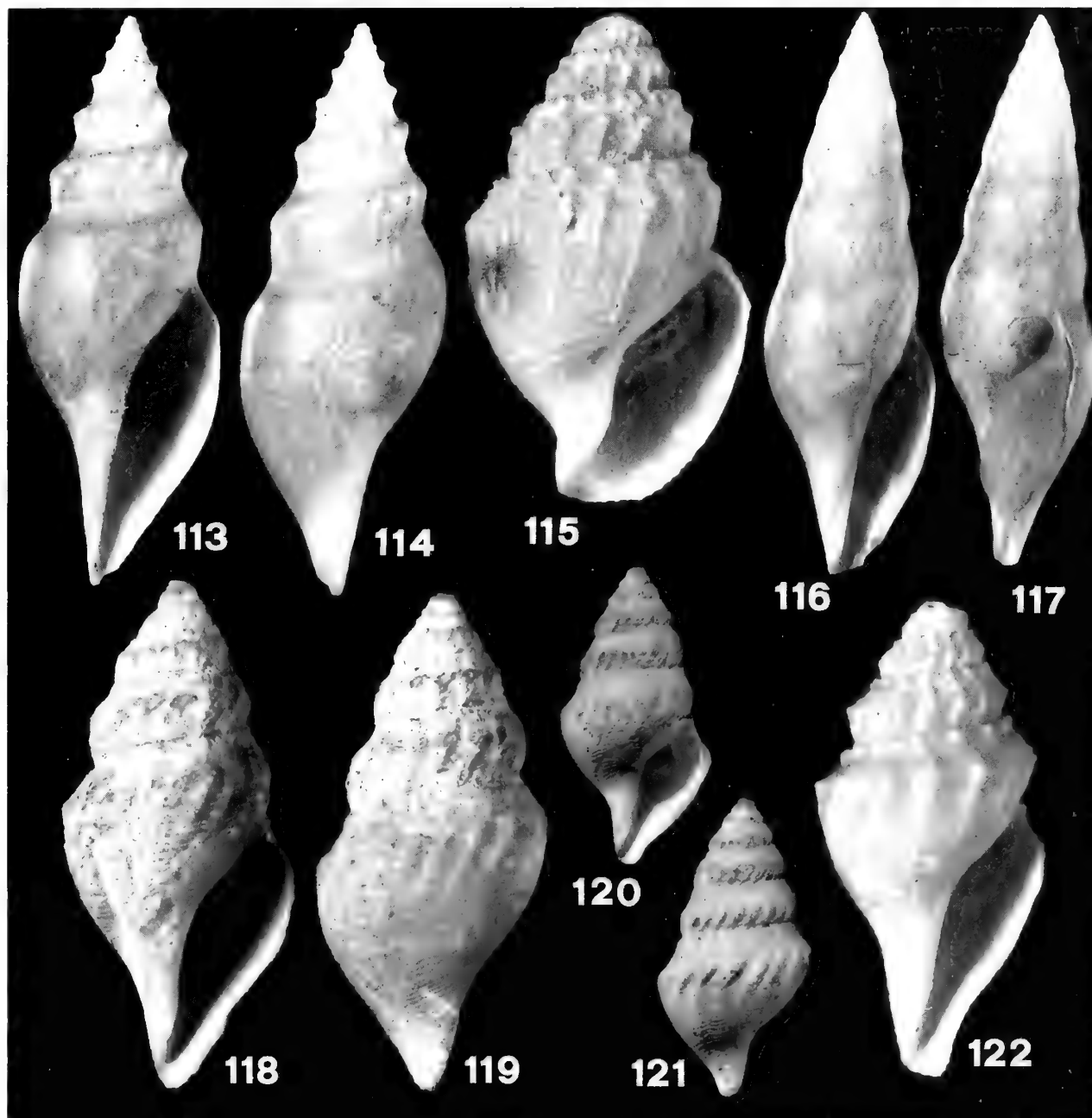
Figs 113 & 114

Mangilia (Spergo) daphnelloides Dall, 1895, p. 683–684, pl. 31, fig. 11.

TYPE LOCALITY. 'Albatross', stn 3476 (Hawaiian Islands), 298 fms.

MATERIAL. stn 118, 1 shell.

The species was originally described within the subgenus *Spergo* which is considered as a full genus by all modern authors. However the species differs from the type species of *Spergo*, *Mangilia (Spergo) glandiniformis* (Dall, 1895), in all important conchological characters included by Dall in the original diagnosis of the subgenus (the latter was based to a considerable extent on the soft body characteristics which are presently treated as insignificant for taxonomy at the generic level), i.e. in having well developed sculpture and rather deep anal sinus. On the other hand, the species is very similar to the group of species assigned by Bouchet & Warén (1980) to the genus *Theta*. The



Figs 113–122 Daphnellinae and Mangeliinae. **113, 114** – *Gymnobela (Theta) daphnelloides* (Dall, 1895), stn 118, H = 27.0; **115** – *Mioawateria extensaeformis* (Schepman, 1913), stn 26, H = 9.9 mm; **116, 117** – *Xanthodaphne maldivica* Sysoev, new species, holotype; **118–121** – *Benthomangelia brachytoma* (Watson, 1881), stn 119, H = 17.1 mm (**118, 119**) and lectotype, BM(NH) 1887.2.9.1034, H = 15.1 mm (**120, 121**); **122** – *B. trophonoidea* Thiele, 1925, stn 185, H = 10.0 mm.

latter, in its turn, is too poorly distinguished from *Gymnobela* to warrant a generic status and should be regarded as a subgenus.

DISTRIBUTION. Hawaiian Islands and East Africa, 545–1789 m. The present record is a great range extension for the species.

Genus *MIOAWATERIA* Vella, 1954

Type species: *Awateria personata* Powell, 1954 (original designation)

Mioawateria extensaeformis (Schepman, 1913)

Fig. 115

Pleurotomella extensaeformis Schepman, 1913, p. 446, pl. 30, fig. 5.

Gymnobela extensaeformis (Schepman) – Thiele, 1925, p. 490(224), pl. 41(29), fig. 9.

Magnella extensaeformis (Schepman) – Shuto, 1971, p. 15–16, pl. 2, figs 10–12.

TYPE LOCALITY. 'Siboga', stn 212, Banda Sea, 462 m.

MATERIAL. stn 26, 2 specimens.

Of the two specimens available ($H = 9.9$ and 6.3 mm, both without protoconch), the smaller is comparable in size to those illustrated by Schepman (8.5 mm, or 8.0 mm according to Shuto, 1971) and Thiele (6.25 mm) and quite similar to them. The larger specimen (Fig. 115) differs in having a broader canal, less excavated subsutural slope, and much weaker peripheral spiral keel on the body whorl. The spiral sculpture of both specimens is subobsolete on the body whorl periphery and upper part of the shell base becoming stronger towards the canal. This is in contrast to both Schepman's and Thiele's figures, but agrees well with Shuto's (1971) illustration of the holotype.

The same species was probably figured by Thiele (1925) as the North-Atlantic *Gymnobela extensa* (Dall, 1881). Thiele's figure, apparently based on a specimen from Sumatra, differs from his illustration of *M. extensaeformis* in having obsolete spiral ribs on the body whorl except for those on the lower shell base and canal, but, as mentioned above, this is the feature characteristic of *M. extensaeformis*.

Recently this species was assigned by Shuto (1971) to *Magnella* Dittmar, 1960. Later, Maxwell (1988) synonymized the latter genus with the New Zealand genus *Mioawateria* Vella, 1954. This synonymization seems to be reasonable, though the status of *Mioawateria* itself remains somewhat uncertain due to great similarity to *Gymnobela* Verrill, 1884. The main difference between two latter genera is the shape of anal sinus which is very shallow in *Mioawateria*. At the same time, the shape of sinus in *Gymnobela* is rather variable, and there are species, traditionally included into *Gymnobela*, quite comparable to *Mioawateria* in this character (e.g. *G. blakeana* (Dall, 1881)). Thus, after comparative examination of broad range of *Gymnobela* species in respect to the anal sinus shape, *Mioawateria* may be either a large and very widely distributed genus or a synonym of *Gymnobela*.

DISTRIBUTION. East Africa (Gulf of Aden to Kenya), Sumatra, Banda Sea, 439–2312 m. The present record is the deepest one.

Genus *XANTHODAPHNE* Powell, 1942

Type species: *Pleurotoma* (*Thesbia*) *membranacea* Watson, 1886 (original designation)

Xanthodaphne maldivica Sysoev, new species

Figs 116 & 117

MATERIAL. stn 143, 1 specimen (holotype No. 1993116).

DESCRIPTION. The shell is narrowly fusiform, slender, thin but solid, light-brown, with glossy surface, consists of the protoconch and 9 teleoconch whorls. The protoconch is partly broken off, but the remaining 1.5 whorls are covered with the typical diagonally cancellated sculpture. The teleoconch whorls are slightly concave in the upper part and weakly convex below. Early teleoconch whorls are angled in the lower part just near the suture, this angulation rapidly shifts upwards and becomes less prominent and practically disappears on the 6th whorl. There is a weak subsutural fold on initial teleoconch whorls. The sutures are very shallow, distinct, and more or less straight. The growth lines are clear, thin, numerous, and strongly curved. The sculpture is represented only by low, wide ribs on the canal; these rapidly become obsolete on the shell base. The shell base is weakly convex and smoothly passes into the canal. The canal is

straight, not differentiated from narrow aperture. The inner lip is covered with a very weak callus which becomes thicker towards the canal extremity. The anal sinus is wide and moderately deep, subsutural, 'reversed L'-shaped, its deepest part is situated just below the suture. The outer lip strongly projects forward below the sinus. $H = 29.0$, $H_b = 17.1$, $H_a = 14.3$, $D = 9.0$ mm.

The new species differs from all known species of the genus in its slender and narrow shell almost completely devoid of spiral sculpture.

DISTRIBUTION. Maldive Islands, 797 m.

Subfamily **MANGELIINAE** Fischer, 1883

Genus *BENTHOMANGELIA* Thiele, 1925

Type species: *Surcula trophonoidea* Schepman, 1913 (original designation)

Benthomangelia brachytoma (Watson, 1881)

Figs 118–121

Pleurotoma (*Drillia*) *brachytoma* Watson, 1881, p. 415.

Pleurotoma (*Spirotropis*) *brachytoma* Watson – Watson, 1886, p. 324–325, pl. 18, fig. 3.

TYPE LOCALITY. 'Challenger', stn 191, off the Arrou Island, south-west of Papua, 800 fms.

MATERIAL. stn 119, 1 shell.

The specimen from the stn 119 ($H = 17.1$ mm) is quite similar to Watson's illustration and to the photograph of one of two syntypes (which should be designated as lectotype) (Figs 120 & 121, $H = 15.3$ mm according to Watson) (the second syntype is represented by broken and heavily worn shell) stored in the NHM. It differs from the lectotype only in more slender shell ($H/D = 2.20$ vs. 2.03 (Watson's measurements) or 1.96 (measured by the photograph) in Watson's specimen) with fewer axial folds.

DISTRIBUTION. East Africa and Indonesia, 1463 and 1207–1463 m.

Benthomangelia trophonoidea (Schepman, 1913)

Fig. 122

Surcula trophonoidea Schepman, 1913, p. 62(426)–63(427), pl. 28, fig. 3.

Mangelia (*Benthomangelia*) *trophonoidea* (Schepman) – Thiele, 1925, p. 190(224)–191(225), pl. 27(39), fig. 25, text-fig. 25.

Benthomangelia trophonoidea (Schepman) – Okutani, 1966, p. 23, text-fig. 11.

?*Marshallena gracilispira* Powell, 1969, p. 370–371, pl. 281, fig. 2.

TYPE LOCALITY. 'Siboga', stn 45, Flores Sea, 794 m.

MATERIAL. stn 185, 1 shell.

The shell from the JME material is small ($H = 10.0$ mm, which is smaller than all the previously recorded specimens, i.e. 16 mm (Schepman), 15.9 mm (Thiele, measured by the figure), and 15.5 mm (Okutani, measured by the figure)) and apparently rather young. It differs from the original description and figure in having prominent tubercles on the subsutural fold of all the shell whorls and in less curved and more developed axial ribs on the subsutural slope. The presence of short plicae on early whorls,

which disappear towards the body whorl, was mentioned by Shepman for the much larger paratype. The prominent axial ribs on the subsutural slope are seen in Thiele's figure of the species. Judging from the published figures of *B. trophonoidea*, the species is rather variable, though it can be mentioned that the proportions of the shell (H/D and Hs/H) are rather constant in different specimens. Thiele's figure illustrates a somewhat more slender shell with better differentiated and more straight siphonal canal and much longer axial ribs, almost reaching the canal (they do not reach the whorl periphery in the holotype). Okutani published an illustration of a shell with a high and narrow spire. However, the variability of *B. trophonoidea* does not exceed that of the Atlantic representatives of the genus (Bouchet & Warén, 1980).

Marshallena gracilispira Powell, 1969, described from Borneo and Philippines, 558–717 m, is probably a synonym of *B. trophonoidea*; from both original description and figure it is impossible to find any essential characters distinguishing the former species from the latter. However, this question cannot be resolved without an examination of type specimens and more material.

DISTRIBUTION. Gulf of Aden, Indonesia, and southern Japan, 660–2000 m. The present record is the most western and most deep-sea locality.

The following species were also mentioned from the John Murray Expedition bathyal samples by A.W.B. Powell (1964, 1969) but not found in the material studied:

Lucerapex denticulata (Thiele, 1925) – Powell, 1964, p. 286 (stn 176, Gulf of Aden, 732 m; stn 184, Gulf of Aden, 1270 m).

Nihonia circumstricta (von Martens, 1901) – Powell, 1969, p. 334 (stn 110, off Pemba Id., 333 m).

Leucosyrinx julia Thiele, 1925 – Powell, 1969, p. 338 (stn 34, Gulf of Aden, 1040 m).

Typhlosyrinx vepallida (von Martens, 1902) – Powell, 1969, p. 360 (stn 184, Gulf of Aden, 1270 m).

Marshallena philippinarum (Watson, 1882) – Powell, 1969, p. 369–370 (three stations without numbers indicated, Gulf of Aden and off Pemba Id., 1061, 1022, and 802 m).

DISCUSSION

A total of 50 species of deep-sea conoidean gastropods were found in the JME collection. They belong to 3 families, 6 subfamilies, 22 genera and 3 subgenera. Lower conoideans (families Drilliidae and Turridae) prevail in the material: 30 species vs. 20 in Conidae. Among subfamilies, the most species-rich appeared to be Cochlespirinae (9 species) and Clathurellinae (11 species).

The material studied seemingly does not represent well the fauna of the North-Western Indian Ocean; this is evidenced by low percentage of small species and juvenile individuals of larger species as compared, for example to East African bathyal fauna described by Thiele (1925). This is probably due to methods of collection. Additional evidence for this may be the very high share of lower conoideans, often represented by large species, (60%) which far exceeds the respective values for East African fauna (about 41%, calculated from Thiele's (1925) list) and for other world-wide faunas (Sysoev, 1991).

Nevertheless, some remarks on the JME collection can be made. The fauna has a typical bathyal appearance, with only few

representatives of characteristic shallow-water (e.g. *Drillia*) and abyssal (e.g. *Gymnobela* (*Theta*) genera).

The high percentage of new species in the material studied (about 1/3) indicates that the North-Western Indian Ocean is still insufficiently explored. This is additionally confirmed by the very low overlap with faunal lists obtained by other expeditions: for example, only 5 out of 59 bathyal species reported by Thiele (1925) for East Africa were found in the JME collection (plus 4 species recorded by Powell – see above); the same is true for the bathyal fauna of Southern India collected by the 'Investigator' (7 species found out of 37 reported by Winckworth, 1940).

Most species were found at only one station, and thus the main areas covered by the JME investigations (i.e. Gulf of Aden, Zanzibar area, and Maldiv Islands) have very few common species: 2 species (*Comitas subsuturalis* and *Gemmula amabilis*) were found in all three areas, 2 species (*Gemmula bisinuata*) and *Borsonia symbiophora* – in the two first regions, and one species (*Comitas erica*) – in the two last. All species also found outside the region studied are apparently widely distributed in the Indo-Pacific. Of particular interest in this connection are the findings which greatly extend the geographic range of respective species: *Horaiclavus splendidus* previously known from Japan, *Leucosyrinx claviforma* from North-Western Australia, and *Gymnobela daphnelloides* from Hawaii.

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Reassessment of '*Calcinus*' *astathes* Stebbing, 1924 (Crustacea: Anomura: Paguridea: Diogenidae)

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SYNOPSIS. A reexamination of the syntypes of '*Calcinus*' *astathes* Stebbing, 1924 in the collection of The Natural History Museum, London, U.K., has shown that although subsequently assigned correctly to the genus *Clibanarius*, this taxon is not conspecific with *C. virescens* Krauss, 1843, as was previously proposed at that time. *Clibanarius astathes* is redescribed and illustrated; a lectotype is designated.

INTRODUCTION

Stebbing (1924) described a new species of hermit crab from Delagoa Bay, South Africa, which he mistakenly assigned to *Calcinus* Dana, 1851. The fact that this species clearly should have been placed in *Clibanarius* Dana, 1852 was recognized by Barnard (1947); however, at that time he made only the notation that four specimens returned to the South African Museum by Stebbing were indistinguishable from *Clibanarius virescens* (Krauss, 1843). Barnard (1950) went on to define those four specimens further by commenting, 'I would not have ventured to dispute the identity of Stebbing's *Calcinus astathes* if there had not been four specimens returned to the Museum bearing Stebbing's autographic label (the largest and type specimen probably retained by him, or perhaps now transferred to the British Museum). These four specimens are obviously *C. virescens*. The dactyl of the 3rd leg is not longer than 6th joint, and has the characteristic shape'.

Stebbing's (1924) original description of *Calcinus astathes* specified only a 'group' of specimens collected from Delagoa Bay by K.H. Barnard on October 12, 1912. Five specimens, listed as syntypes of this taxon are part of the Stebbing Collection donated to The Natural History Museum (NHM) [formerly British Museum (Natural History)] by Barnard, although only three initially were listed in the Museum registry (NHM 1928.12.1.264–266). Four specimens, dry, and in poor condition, remain in the collection of the South African Museum (SAM) catalogued under the original number (A2121)

listed by Stebbing (1924). Barnard's hand written label accompanying the dry specimens reads 'A2121. Delagoa Bay 4 spec. returned by Stebbing labelled (*sic*) as '*Calcinus astathes*' also 1 with parasites see Stebbing, 1920'. Barnard's label reference to the parasitized specimen must refer to a specimen without chelipeds included by Stebbing (1920), with others (NHM 1928.12.1.267–268, SAM A3270 A2120), identified as *Calcinus laevimanus* (Randall, 1840), the former specimen similarly placed in synonymy with *C. virescens* by Barnard (1950: 435). No specimens of *Calcinus* or *Clibanarius astathes* were listed among the type collection in the South African museum by Kensley (1974), and none have been found on a recent search (Ms. L. Hoenson, pers. comm.).

Despite some confusion in the initial NHM registry entry for '*Calcinus*' *astathes*, at least two points are clear. These five specimens labeled as syntypes of Stebbing's (1924) species all belong to the same taxon; none are conspecific with *Clibanarius virescens*. The four specimens remaining in the SAM collection truly do represent *C. virescens*. The largest of the NHM specimens [and the one presumably unaccounted for by Barnard (1950)] is herein designated as the lectotype of '*Calcinus*' *astathes*.

MATERIAL AND METHODS

In addition to the syntypes, and Barnard's four specimens of *Clibanarius virescens*, comparative material of a

morphologically similar *Clibanarius* species, *C. longitarsus* (De Haan, 1849) from Durban Bay, S.A., has been examined. One measurement, shield length (SL), measured from the tip of the rostrum to the midpoint of the cervical groove provides an indication of specimen size. The type material of *C. astathes* has been returned to the Natural History Museum, and Barnard's *C. virescens* to the South African Museum. Two specimens of *C. longitarsus* used in the comparison also have been deposited in The Natural History Museum (NHM 1995.163–164), the remaining have been retained in the author's personal collection.

SYSTEMATIC ACCOUNT

Clibanarius astathes (Stebbing, 1924)

Figs 1, 2

Calcinus astathes Stebbing, 1924: 239, pl. 2 (CXVII of continuing series). *Clibanarius virescens*: Barnard, 1947: 376 (in part); 1950: 435 (in part). Lectotype (herein selected). Female (SL = 7.3 mm), NHM reg. 1928.12.1.264 Paralectotypes. Two females (SL = 6.3, 6.3 mm), 2 males (SL = 5.8, 6.9), NHM reg. 1928.12.1.265–266.

TYPE LOCALITY. Delagoa Bay (25°50'S, 32°50'E), 'Mosambique', Ethiopian region, Indian Ocean, 1912.

DIAGNOSIS. Rostrum with simple or bifid termination. Ocular peduncles 0.66–0.75 length of shield; little if at all overreached by antennular peduncles; antennal peduncles not reaching to bases of corneae. Ocular acicles with acute, simple or bifid termination. Basal segment of antennular peduncle with 1 or 2 small spines.

Chelipeds subequal, right somewhat larger. Right cheliped with dactyl equal to or slightly longer than palm; dorsomesial margin and dorsal surface with rows of corneous-tipped spines. Dorsomesial margin of palm with row of low spines and tufts of long setae, second adjacent row of spines and one large tubercle at proximal margin, dorsal surface sloping, with few spines distally and on proximal portion of fixed finger. Dorsomesial distal angle of carpus with acute spine, low protuberances and tufts of setae on dorsomesial margin. Merus with few low, somewhat spinulose protuberances on ventromesial margin; ventrolateral distal angle with three acute spines. Left cheliped with few more spinules on dorsal surface of palm. Carpus with two strong corneous-tipped spines on dorsomesial margin and blunt protuberance in line with tubercle on proximal margin of palm. Ventromesial margin of merus with row of few small spines or two small spines distally; lateral face with two spines at ventrolateral distal angle.

Ambulatory legs similar from left to right. Dactyls approximately 1.5 times longer than propodi; dorsal surfaces flattened; ventral margins each with row of minute corneous spinules (10–13 in distal half and one or two proximally). Lateral faces of propodi each with very strongly developed dorsolateral margin; dorsal surfaces somewhat flattened; ventrolateral distal angles each with one or two spines. Carpi each with spine at dorsodistal angle. Meri each with acute spine at ventrolateral distal angle. Sternite of third pereopods with subrectangular anterior lobe, anterior margin slightly rounded. Fourth pereopods each with acute spine at dorsodistal margin of carpus.

Telson with slightly asymmetrical posterior lobes, separated

by small median cleft; terminal margins each with three to five small spines, larger on left.

REDESCRIPTION

Shield longer than broad; anterior margin between rostrum and lateral projections straight or very faintly concave; anterolateral margins sloping; posterior margin roundly truncate. Dorsal surface of shield with scattered setae and distinct 'Y'-shaped suture medianly in posterior portion. Rostrum triangular, terminating acutely or minutely bifid, overreaching lateral projections. Lateral projections broadly rounded or obtusely triangular, with terminal spinule or blunt small projection.

Ocular peduncles slender, 0.66–0.75 length of shield, with scattered setae dorsally and mesially; corneae not dilated. Ocular acicles narrowly triangular, dorsally rounded (convex), with simple or bifid acute termination; separated by less than basal width of one acicle and tending to become approximate distally.

Antennular peduncles overreaching distal margin of corneae little if at all. Ultimate and penultimate segments with scattered setae. Basal segment with one or two very small spinules on ventrolateral distal margin.

Antennal peduncles reaching approximately to bases of corneae; with supernumerary segmentation. Basal segment without spine on laterodistal margin, but with acute spine on ventrodistal margin laterally. Second segment with dorsolateral distal angle produced, with small terminal spine, dorsomesial distal angle rounded. Third segment with small spine on ventrodistal margin. Fourth and fifth segments with scattered setae. Antennal acicle reaching almost to distal margin of fourth peduncular segment, triangular, armed on mesial margin with one to three spines and tufts of setae, terminating in acute spine. Antennal flagellum overreaching chelipeds, and approximately as long as ambulatory legs; each article with two or three minute bristles.

Chelipeds subequal, right somewhat larger. Right cheliped with dactyl equal to or slightly longer than palm; dorsomesial margin with row of corneous-tipped spines, dorsal surface with two rows of appreciably stronger, corneous-tipped spines; surfaces all with numerous tufts of moderately long setae; cutting edge with two prominent calcareous teeth in proximal half and broad terminal corneous hoof-shaped claw. Palm slightly longer than carpus; dorsomesial margin with row of low spines and tufts of long setae, second adjacent row of spines and one large tubercle at proximal margin, dorsal surface sloping, with no delimitation of dorsolateral margin, surface with few spines distally and on proximal portion of fixed finger, also with tufts of long setae; fixed finger with two rows of small spines on dorsal surface, all surfaces with tufts of long setae; cutting edge with three calcareous teeth in proximal half, distal-most strongest; terminating in corneous hoof-shaped claw. Carpus slightly more than half length of merus; dorsomesial distal angle with acute spine, low protuberances and tufts of setae on dorsomesial margin; dorsal surface with indications of points of original tufts of setae (no longer present), dorsolateral margin not delimited; mesial face with few scattered tufts of setae. Merus subtriangular; dorsal margin with tufts of setae; ventromesial margin with few low, somewhat spinulose protuberances and tufts of setae; ventrolateral distal angle with three acute spines, ventrolateral margin proximally and lateral

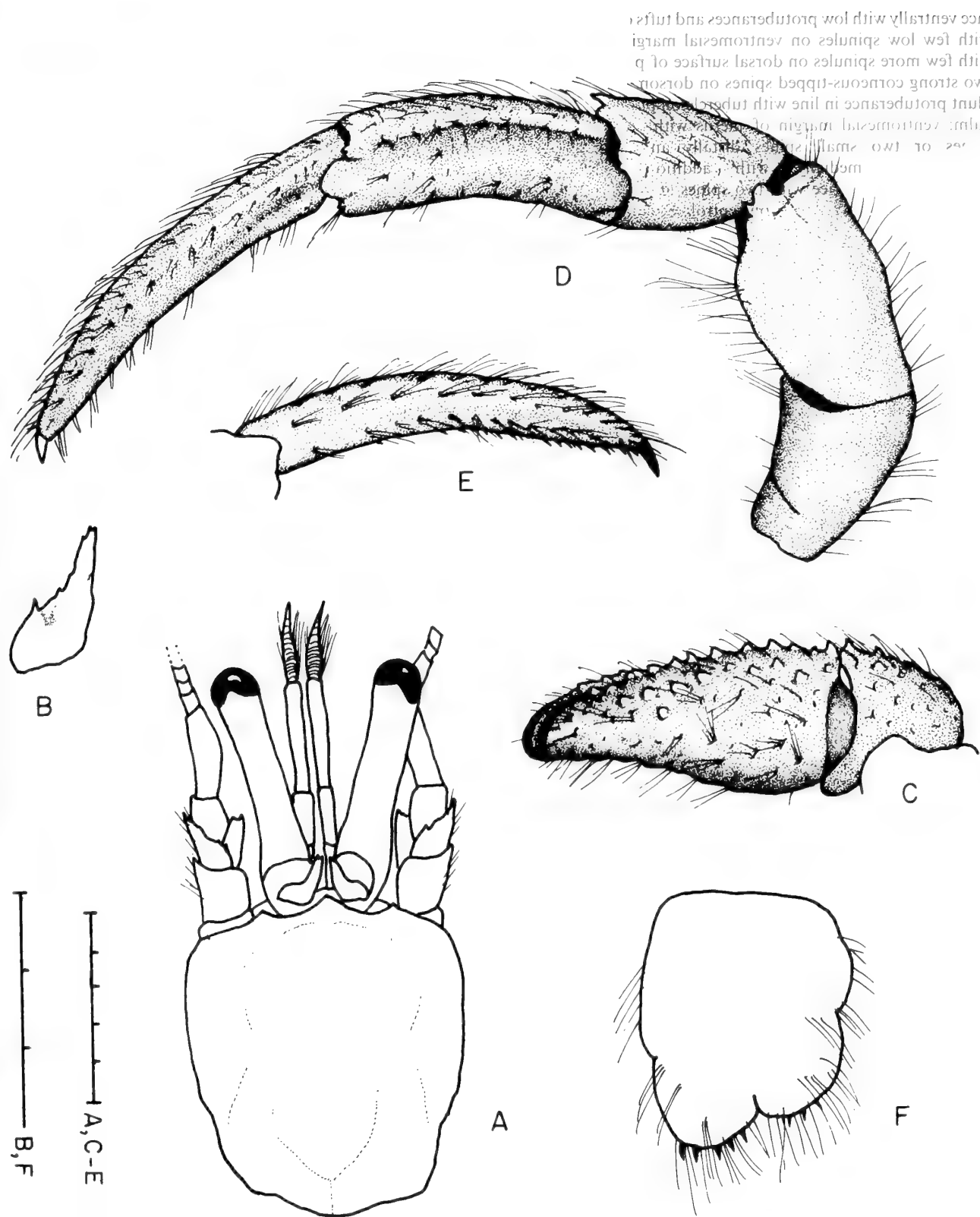


Fig. 1 *Clibanarius astathes* (Stebbing, 1924), A-E, female lectotype (7.3 mm); F, male paralectotype (6.9 mm). A, shield and cephalic appendages; B, right second antennal peduncular segment enlarged; C, carpus and chela of left cheliped (lateral view); D, third left pereopod (lateral view); E, dactyl of third left pereopod (mesial view); F, telson. Scales equal 5.0 mm (A, C-E) and 3.0 mm (B, F).

face ventrally with low protuberances and tufts of setae. Ischium with few low spinules on ventromesial margin. Left cheliped with few more spinules on dorsal surface of palm; carpus with two strong corneous-tipped spines on dorsomesial margin and blunt protuberance in line with tubercle on proximal margin of palm; ventromesial margin of merus with row of few small spines or two small spines distally and two, plus low protuberance, medially, with additional protuberance proximally; lateral face with two spines at ventrolateral distal angle and low protuberances on ventrolateral margin.

Ambulatory legs similar from left to right. Dactyls approximately 1.5 times longer than propodi; in dorsal view straight, in lateral view slightly curved; dorsal surfaces flattened, and with rows of tufts of stiff setae, lateral faces each with longitudinal row of tufts of stiff setae; ventral margins with row of tufts of stiff setae and row of minute corneous spinules, 14 (spaced distally to proximally 8,5,1) on left third (lectotype), right third with 10, left second with 13, all in distal half; paralectotypes usually with 10–13 spinules in distal half and one or two proximally. Propodi slightly less than twice length of carpi; lateral faces each with distinctly developed dorsolateral margin and tufts of setae; dorsal surfaces somewhat flattened and with numerous tufts of setae; ventrolateral distal angles each with one or two spines, ventral margins with tufts of setae. Carpi 0.66 to 0.90 length of meri; each with spine at dorsodistal margin and tufts of setae on dorsal and lateral faces. Meri with tufts of setae dorsally and ventrally; ventrolateral distal angles each with one acute spine and ventral margins of second also with low protuberances. Ischia with tufts of setae on ventral margins. Fourth pereopods each with acute spine at dorsodistal margin of carpi. Sternite of third pereopods with subrectangular anterior lobe, anterior margin slightly rounded. Uropods asymmetrical. Telson with transverse suture; posterior lobes slightly asymmetrical, separated by small median cleft; terminal margins each with three to five small spines, larger on left.

COLOUR. Unknown.

DISTRIBUTION. At present recognized only from the type locality, Delagoa Bay, South Africa.

AFFINITIES. *Clibanarius astathes* shares with *C. padavensis* De Man, 1888, dactyls of the ambulatory legs that are longer than the propodi. Barnard (1926) listed the latter species from Delagoa Bay, and subsequently (Barnard, 1950) gave a brief diagnosis of that species. The ratio of cornea diameter to ocular peduncle length cited by Barnard is less than that given by De Man (1888) in his original description, or later by Alcock (1905), and the illustrated propodus of the left third pereopod (Barnard, 1950: fig. 80d) is appreciably shorter and stouter than that described for *C. padavensis*. However, if the colour patterns described by Barnard actually were taken from his specimens, one must assume that his identification was correct, and that *C. astathes* and *C. padavensis* exist sympatrically in the Delagoa area.

I have not had the opportunity to examine Barnard's (1950) specimen(s) of *C. padavensis*, nor other specimens of this species; however, De Man's (1888) very detailed description points to several characters that would distinguish *C. padavensis* from *C. astathes* in the absence of colour. These include longer and more slender ocular peduncles; multispinose ocular acicles; longer antennal acicles, which reach beyond the proximal margins of the penultimate peduncular segments; longer and more slender chelae; and subcylindrical propodi of the ambulatory legs.

Clibanarius astathes also bears a very strong resemblance to *C. longitarsus*. *Clibanarius astathes* differs from the Durban Bay population of *C. longitarsus* (12 males, 3 females, SL = 1.9–10.4 mm) that I have examined, in having: 1) fewer spines on the ventrolateral distal margin of the antennular peduncle (one or two, as opposed to three to six in *C. longitarsus*); 2) two strong corneous-tipped spines on the dorsomesial margin of the carpus of the left cheliped (only one was observed in numerous specimens of *C. longitarsus* of varying sizes); 3) strongly delineated dorsomesial propodal margin on the third pereopod (rounded or very faintly ridged in *C. longitarsus*); 4) roundly rectangular anterior lobe on the sternite of the third pereopods (this lobe is subquadrate, and often with a central blister-like protuberance in *C. longitarsus*). Other characters, such as the rows of spines on the fixed finger of the left cheliped, the armature of the ventral margins of the meri of the chelipeds, the

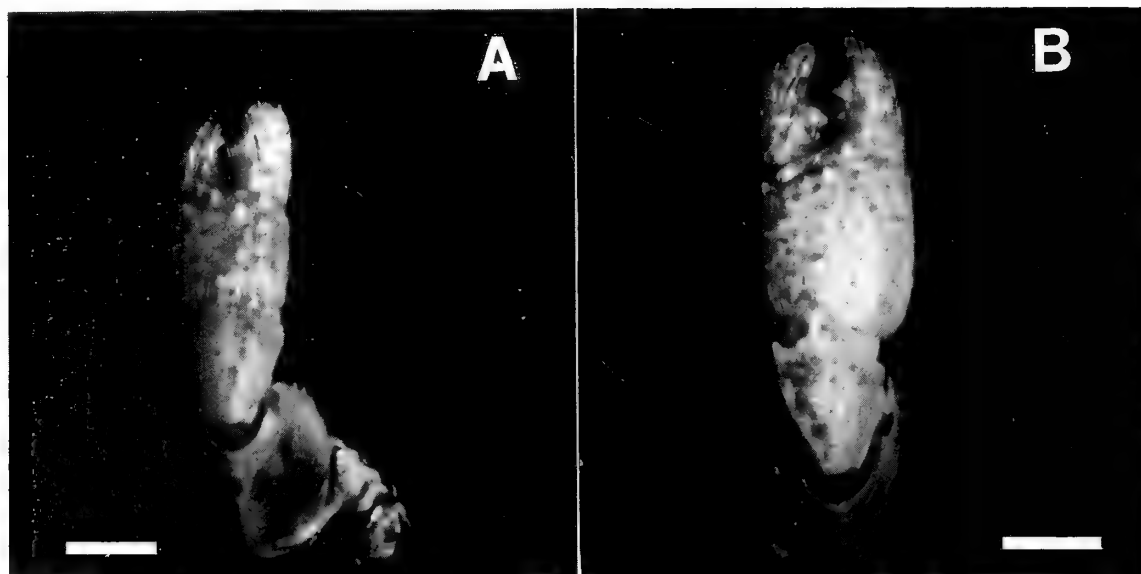


Fig. 2 *Clibanarius astathes* (Stebbing, 1924), male paralectotype (6.9 mm). A, left cheliped; B, right cheliped. Scale equals 12 mm.

presence of a spine at the ventrolateral distal angle of the merus of the third right and left pereopods, the number and spacing of the corneous spinules on the ventral margins of the ambulatory dactyls, and the spination of the terminal margins of the telson appear quite variable in *C. longitarsus*. Too few specimens of *C. astathes* are known for any evaluation of morphological variation.

REMARKS. Stebbing's (1924) comments on the genus *Calcinus* emphasized as did his earlier remarks (Stebbing, 1914), the development of the maxillipeds, which seems to suggest that he was not really familiar with the overall morphology of *Calcinus* species. Finding similar maxillipedal development in his new taxon, Stebbing (1924) assigned *astathes* to this genus, with apparent disregard for the numerous characters which set *Clibanarius* apart from *Calcinus*.

It also would appear that the telson of the specimen he described and illustrated (Stebbing, 1924: 240, pl. 2T) was not closely examined, as it was characterized and depicted as being a simple plate with a smoothly rounded terminal margin. In actuality, the telson has a slight transverse suture dividing it into anterior and posterior lobes; the posterior lobes are separated by a small median cleft, and the terminal margins each have a few distinct spines.

Barnard (1950) was correct to transfer Stebbing's (1924) taxon to *Clibanarius*, although this transfer was obscured by his placement of the species in synonymy with *C. virescens*. *Calcinus astathes* Stebbing, 1924 was still listed by Gordan (1956) in her comprehensive tabulation of hermit crab species, and more recently was included by Morgan (1991) in his world-wide listing of known *Calcinus* species. Barnard's (1950) decision regarding the conspecificity of *Clibanarius astathes* and *C. virescens* appears to have been based on specimens incorrectly labeled by Stebbing, and not on the actual type material of *C. astathes*. Not only the fact that the Natal-Mozambique areas of South Africa are type localities of both species, but also the inadequacy of Stebbing's (1924) original description and illustrations, undoubtedly account for Barnard's (1950) synonymy having been accepted, without question, by subsequent carcinologists.

One of the principal characters upon which Barnard (1950) based his identification of *C. virescens* was the shortness of the dactyls of the third pereopods in relation to the propodi, although, as pointed out by Lewinsohn (1982), this character was not mentioned in Krauss' (1843) original description of the species. Not only Barnard (1950), but Fize and Serène (1955), and Gherardi and McLaughlin (1994) reported that the dactyls of their specimens were shorter than the propodi; however, Buitendijk (1937), Miyake (1978), and Lewinsohn (1982) described the dactyls and propodi as being equal in length. Rahayu and Forest (1993) found the dactyls longer than the propodi in small specimens, but shorter in large specimens. Stebbing (1924), like Krauss (1843), made no mention of the length ratios of the dactyls and propodi of the ambulatory legs of *C. astathes*.

Despite the variations in this major diagnostic character observed in *C. virescens*, *C. astathes* sensu stricto differs markedly from Krauss' (1843) taxon. The dactyls of the ambulatory legs of *C. astathes* are approximately half again the length of the propodi. Additionally, the ventral margins of the ambulatory dactyls are armed with 10 to 14 tiny corneous spinules in *C. astathes*, in contrast to the five to eight strong corneous spines seen in *C. virescens*. As previously indicated, *C. astathes* bears a far greater similarity to that group of

Clibanarius species characterized by long pereopodal dactyls and very short antennal acicles.

ACKNOWLEDGEMENTS. I am indebted to Paul Clark, The Natural History Museum, London, for the loan of Stebbing's syntypic material, and to Barbara Cook and Liz Hoenson, South African Museum, Cape Town, for providing the specimens upon which Barnard based his synonymy. The photographs are to work of E.J. McGeorge. This a scientific contribution from the Shannon Point Marine Center, Western Washington University.

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On a new species of *Ophidiaster* (Echinodermata: Asteroidea) from southern China

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SYNOPSIS. A new species, *Ophidiaster multispinus*, from southern Chinese waters, is described. This was previously recorded by A.M. Clark (1982) and by Liao & Clark (in press) as *Ophidiaster armatus* Koehler, 1910 but both authors now believe that Chinese specimens are specifically distinct.

SYSTEMATIC DESCRIPTION

Family OPHIDIASTERIDAE

Genus *Ophidiaster* L. Agassiz, 1835

Ophidiaster multispinus sp. nov.

Fig. 1, pl. 1

Ophidiaster armatus: A.M. Clark, 1982:487, 490; Liao & Clark (in press): [Non *Ophidiaster armatus* Koehler, 1910].

HOLOTYPE. IOAS:E1070, Hainan Strait, southern China (20°15'N, 110°15'E), 55 m, rocky, collected July 10, 1960; paratypes IOAS-E-1071, 4 specimens from Xiamen (Amoy), Fujian Province, 1975.

DESCRIPTION. R (major radius) 55–70 mm; r (minor radius) 10 mm, br (arm breadth basally) 11 mm. Disc small, arms five, unequal, cylindrical, only tapering slightly in the distal third to rounded tips. Abactinal plates large, more or less triangular in

shape, slightly convex, covered with numerous coarse granules, density in the central part of the plates 12–18/mm². Abactinal plates on dorsal surface of arms arranged in three regular longitudinal series, together with the two marginal series each side forming seven regular longitudinal series as well as transverse ones. Papular areas distinctly arranged in eight longitudinal series but the lowest on each side with only a few pores in each area. No pedicellariae detected. All the marginals, except the basal three to five, armed with a fairly conspicuous short blunt spine, these forming a longitudinal series but missing on occasional plates, leaving small gaps in the sequence. Some abactinal plates near the arm tips also bearing one or two small spines but these are not at all conspicuous.

Adambulacral plates with two furrow spines, those of consecutive plates not separated by granules on the vertical faces of the furrows. A large cone-like subambulacral spine on each plate, set back from the furrow within the general granulation. The most proximal six to eleven adambulacral plates with a smaller supplemental series of subambulacral spines interposed between the furrow spines and the main subambulacral ones.

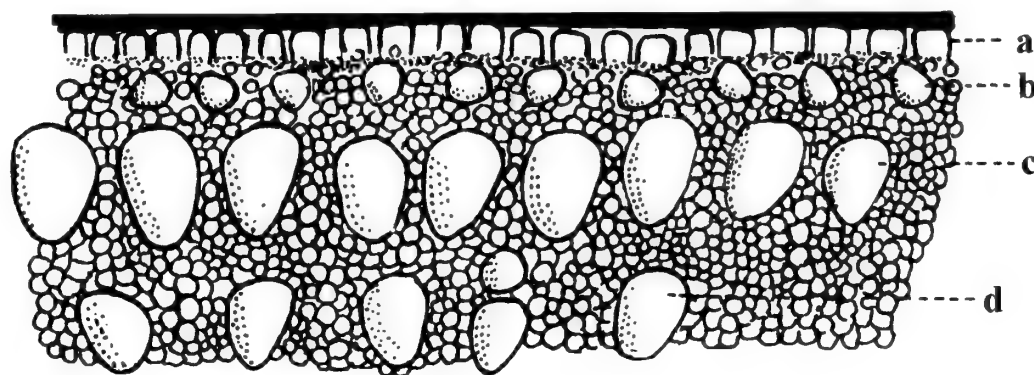


Fig. 1 *Ophidiaster multispinus* sp. nov., Holotype. Proximal portion of actinal surface showing: (a) furrow spines; (b) supplemental subambulacral spines; (c) subambulacral spines; (d) actinal spines. The mouth is towards the right. The scale bar = 2 mm.

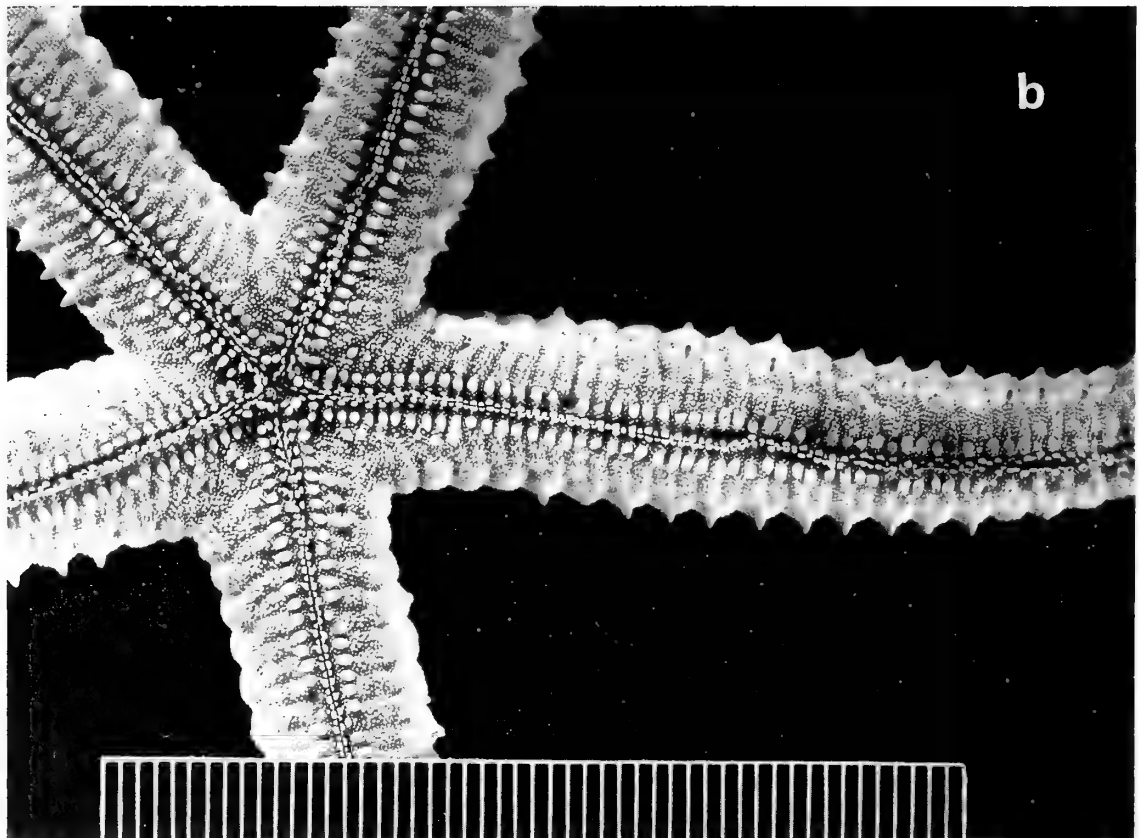
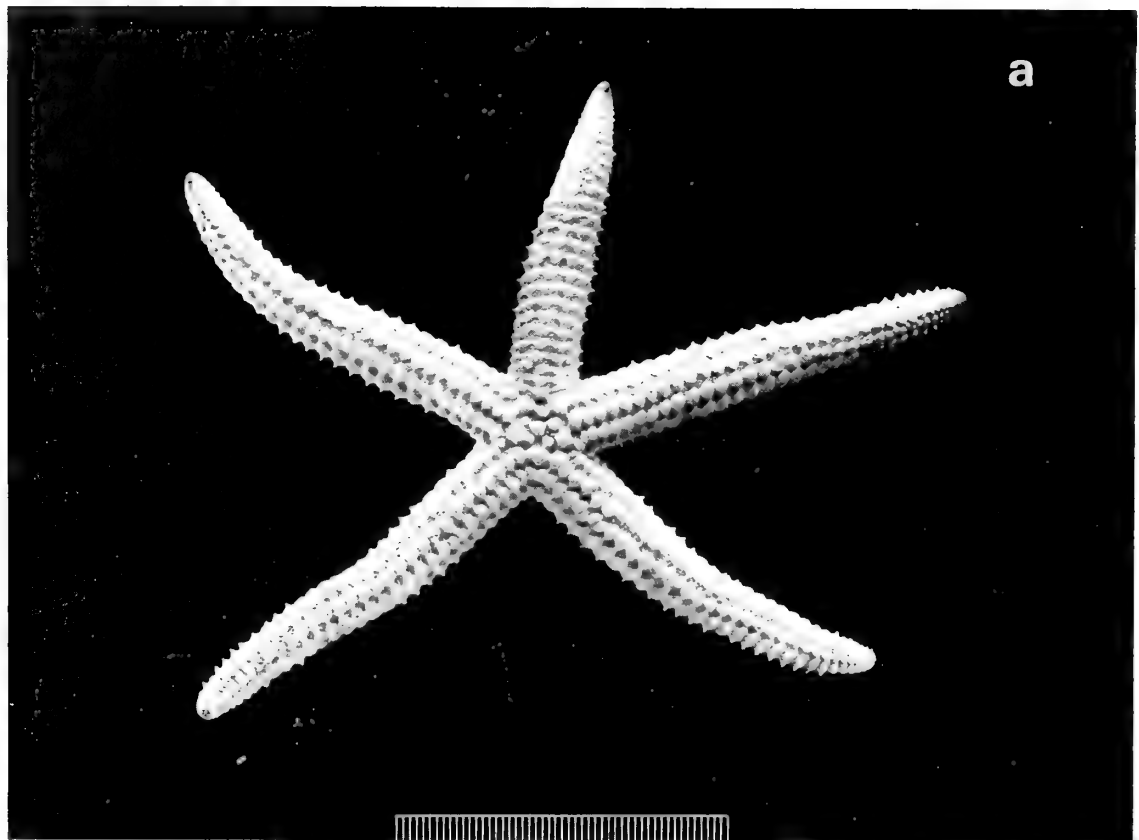


Plate 1 *Ophidiaster multispinus* sp. nov. Holotype: (a) dorsal view; (b) ventral view.

Four or five actinal plates in each intermediate area, armed with single spines corresponding to the subambulacral spines (Fig. 1). Colour (in the dried state) yellowish with faint darker bands.

In addition to the holotype, there are four paratypes from Amoy, Fujian Province, far to the east of Hainan Strait. These are much larger than the holotype (which was selected for better comparison with the type material of *Ophidiaster armatus*) and have R 95, 105, 108 and 115 mm. Three of them have pedicellariae on some abactinal plates.

Four other large specimens (R c. 130 mm), from the east side of Hong Kong Island in c. 15 m, studied by A.M.C., show some variation in the extent of the marginal spines, which are most numerous on the inferomarginals and may extend almost to the interradius.

REMARKS. This new species was previously referred to *Ophidiaster armatus* Koehler, 1910 by A.M. Clark (1982) and by Liao & Clark in 'The echinoderms of southern China' (in press), both references commenting on the unusually large size. During a visit to the Senckenberg Museum by the senior author in 1993, a direct comparison was made between the small Chinese specimen and the three syntypes of *O. armatus* from the Aru Islands, Indonesia, of similar size. As a result of this comparison, we conclude that the Chinese specimens are specifically distinct, the differences being evident as shown in Table 1.

The maximum size for *Ophidiaster armatus*, R 66 mm, was observed by H.L. Clark (1938) in material from Queensland, Australia.

It is noteworthy that all three syntypes of *O. armatus* do have some abactinal pedicellariae which Koehler seems to have overlooked, however, the occurrence of pedicellariae is rarely regarded as a character of specific weight in this family.

The presence of spines on plates other than the adambulacral, separates *Ophidiaster armatus* and *O. multispinus* from the remaining species of the genus *Ophidiaster*.

Table 1 Comparison between the two species mentioned.

| <i>Ophidiaster multispinus</i> sp. nov. | <i>O. armatus</i> Koehler |
|--|---|
| Maximum R 130 mm. | Maximum R 66 mm. |
| Arms stout, br 11 mm at R 60 mm. | Arms slender, br 9 mm at R 60 mm. |
| Marginal spines fairly conspicuous and more extensive, absent only from the first 3–5 plates | Marginal spines not at all conspicuous, only present towards the arm tips |
| Proximal adambulacral with two series of subambulacral spines | Subambulacral spine series single throughout |
| 4 or 5 spinose actinal plates in intermediate area | No spinose actinal plates |

However, in our opinion, this character is not of sufficient importance to justify a generic distinction, especially as the lesser development in *O. armatus* provides an intermediate condition.

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Comparison between the two species mentioned.

| <i>ter. wulviformis</i> sp. nov. | <i>O. wulvulus</i> Koehler |
|----------------------------------|-----------------------------------|
| um R 130 mm. | Maximum R 66 mm. |
| stout, br 11 mm at R 60 mm. | Arms slender, br 9 mm at R 60 mm. |
| um the first 3-5 plates | towards the arm tips |
| 3 more extensive, present only | conspicuous, only present |
| um spines fairly conspicuous | Marginal spines not at all |
| series of subambulacral spines | single throughout |
| uminal subambulacral with two | subambulacral spine series |
| at 2 spinose actinal plates in | No spinose actinal plates |
| intermediate areas | |

However, in our opinion, this character is not of sufficient importance to justify a generic distinction, especially as the lesser development in *O. wulvulus* provides an intermediate condition.

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The life cycle of *Paracyclops fimbriatus* (Fischer, 1853) (Copepoda, Cyclopoida)

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SYNOPSIS. The complete life cycle of *Paracyclops fimbriatus* (Fischer, 1853) (Copepoda, Cyclopoida) is redescribed based on cultured material. All 6 nauplius and 5 copepodid stages plus the adults are described in detail. Scanning electron microscopy is used to elucidate the fine structure of some appendages, especially the male antennule, and to study body ornamentation patterns. Sexual dimorphism is first apparent at the copepodid IV stage which has a more robust antennule in the male than in the female.

INTRODUCTION

Paracyclops fimbriatus has been reported from a wide range of freshwater habitats and the geographical records summarised by Dussart & Defaye (1985) indicate a cosmopolitan distribution. It has also been regularly recorded from subterranean waters (Itô, 1954; Pesce & Galassi, 1987) and from waters with a salinity of 31‰ (Löffler, 1961). Early reports of this species at great depths in Lake Baikal (Mazepova, 1962) refer to the newly recognized *P. baikalensis* Mazepova, 1978 (Mazepova, 1978).

The genus *Paracyclops* comprises 24 species and subspecies (Dussart & Defaye, 1985; Reid, 1987a, 1987b; Strayer, 1988). The type species, *P. fimbriatus*, was originally described by Fischer (1853), using material from St-Petersburg in Russia. This taxon has been partially redescribed on numerous occasions (for example Kiefer, 1929; Gurney, 1933; Lindberg, 1941; Dussart, 1969; Einsle, 1971). Some descriptions of developmental stages have also been published; one of the most accurate being that of Gurney (1933) but even that gives insufficient data to characterise the copepodid stages. Other descriptions have concentrated primarily on the naupliar instars (Gurney, 1933; Dukina, 1956; Ewers, 1930), but these all lack detail by modern standards. Although the general morphology of cyclopoid naupliar stages has been known for a long time it is only recently that detailed naupliar descriptions of freshwater cyclopoid copepods have been published (Dahms & Fernando 1992, 1993, 1994). Systematic studies on naupliar stages can

provide important information on the phylogenetic relationships among copepods (Dahms, 1991a,b).

In the present paper *P. fimbriatus* has been redescribed in detail, including all its developmental stages, in order to provide a base for comparison with other *Paracyclops* species.

METHODS

Adult females of *P. fimbriatus* were collected by plankton net from Regent's Park pond (London) on 29.5.1994. Ovigerous females were kept in plastic dishes filled with fresh water filtered through a 35 µm-mesh net. Water was changed at 2 day intervals until the eggs hatched and the nauplius phase was completed. The adult females were removed after hatching of their egg sacs. Copepodid stages were placed in an aquarium tank in a constant temperature room.

The nauplii were examined as whole mounts. Broken glass-fibres were used to prevent the nauplii from being compressed by the coverslip and to facilitate rotation which allowed viewing from all sides.

Copepodids were dissected in lactophenol. All drawings were made with the aid of a camera lucida using Nomarski differential interference contrast. All measurements were made with an ocular micrometer. Body lengths were measured from the anterior to the posterior end of the body in nauplii, and from the base of the rostrum to the posterior edge of the caudal rami

in copepodids. Body width is given as the widest part of the nauplius body or the copepodid cephalothorax. In the spine and seta formula of the swimming legs Roman numerals and Arabic numerals are used for spines and setae respectively.

When necessary scanning electron microscopy (SEM) was used to study fine details. Material for SEM was prepared by cleaning specimens in an aqueous solution (one drop in 100 ml of distilled water) of the surfactant detergent RBS pF for 30 min and subsequently sonicating in an ultrasonic cell disrupter for 7 s. Cleaned specimens were washed in 3 changes of distilled water for 5 minutes, dehydrated through a graded acetone series, critical point dried, mounted on aluminium stubs, sputter coated with gold and viewed under an Hitachi S-800 scanning electron microscope.

RESULTS

Description of Naupliar Stages

Nauplius I

Body length : mean \pm standard deviation = $118 \pm 2.68 \mu\text{m}$ (range 113 to 122 μm , $n=20$), mean body width $75 \pm 1.5 \mu\text{m}$ (range 72 to 77 μm , $n=20$). Body oval (Fig. 1A), with posterior spinular row on ventral surface and on either side of caudal setae. Ventral surface with 2 paired patches of spinules posterior to labrum. Oval area of integument located posteriorly on ventral surface. Caudal rami represented by pair of naked setae.

Antennule 3-segmented (Fig. 2A). First segment with 1 spinulose seta anteriorly and group of spinules along outer margin. Second segment with 2 setae, distal one spinulose and slightly shorter than proximal plumose one; ornamented with 2 spinular rows along ventral side. Third segment with 2 naked setae distally and 2 spinular rows along ventral margin.

Antenna biramous (Fig. 3A), with 2-segmented protopod comprising coxa and basis. Coxal gnathobase represented by large spine armed with spinular row distally. Basis with 3 small setae along inner margin, 2 of them closely set together in proximal third. Exopod 4-segmented; segment 1 large with 1 spinulose seta and spinular row on outer margin; second segment with 1 long naked seta; third segment with 1 long naked seta and few tiny spinules on outer margin; fourth segment with naked seta proximally and 1 long spinulose seta plus 1 naked seta distally; outer margin with spinular row near proximal seta and single isolated setule apically. Endopod unsegmented; armed with 2 short inner setae and 2 long setae terminally.

Mandible (Fig. 4A) biramous, with 2-segmented protopod comprising small coxa and large basis. Coxal gnathobase with 1 naked seta. Inner margin of basis with 1 spinulose and 1 naked seta; outer margin with minute spinule. Exopod 4-segmented; first to third segments each with 1 plumose seta at inner distal angle; segments 3 and 4 with spinular row along outer margin; apex of fourth segment with long plumose, inner seta and short, naked, outer seta, the latter about as long as segment. Endopod 2-segmented; first segment with two spinulose setae and spinular row on inner distal margin; second segment with 4 naked setae.

Nauplius II

Body length : mean \pm standard deviation = $135 \pm 7.84 \mu\text{m}$ (range 113 to 144 μm , $n=21$), mean body width $88 \pm 4.5 \mu\text{m}$ (range 83 to 100 μm , $n=21$). Body similar to first nauplius but larger and elongated caudally (Fig. 1B); differing as follows: labrum (Fig.

19C) with some spinules along lateral margin. Caudal region lacking spinular row adjacent to caudal setae.

Antennule (Fig. 2B) armed with third seta on inner terminal edge of distal segment. Antenna (Fig. 3B) with additional small seta at base of large sword-shaped coxal gnathobasic seta. Basis with distal spinular row. Exopod 6-segmented, with 1 extra seta located on minute second segment (arrowed in Fig. 16A). Terminal segment of first nauplius subdivided; segment five with 1 naked seta and additional spinular row distally. Endopod of antenna with 2 plumose setae of equal size and 1 shorter plumose seta terminally, plus 2 inner lateral naked setae.

Coxa of mandible (Fig. 4B) with unilaterally spinulose seta. Additional naked seta present on inner margin of basis. First segment of endopod with one naked seta and one longer plumose seta but with no spinular row on inner distal margin. Second segment of endopod with 4 naked setae and 1 plumose seta. Base of first exopodal segment with additional naked seta.

Maxillule appearing as strong plumose seta (arrowed in Fig. 1B).

Nauplius III

Body length : mean \pm standard deviation = $158 \pm 6.08 \mu\text{m}$ (range 155 to 168 μm , $n=14$), mean body width $105 \pm 8.7 \mu\text{m}$ (range 88 to 117 μm , $n=14$). Body (Fig. 1C) similar to second nauplius but larger, differing as follows: lateral spinular row on labrum consisting of much stronger spinules. Caudal margin with pair of strong plumose setae adjacent to longer naked setae. Posterior end of body trilobate.

Third segment of antennule (Fig. 2C) acquiring extra naked seta on inner margin. Sixth exopodal segment of antenna (Fig. 3C) with 1 naked inner seta, 1 strong spinulose subapical seta and 1 long spinulose apical seta. Mandible with minor changes in relative lengths of endopodal setae (Fig. 4C).

Nauplius IV

Body length : mean \pm standard deviation = $181 \pm 8.4 \mu\text{m}$ (range 166 to 192 μm , $n=14$), mean body width $125 \pm 8.7 \mu\text{m}$ (range 113 to 144 μm , $n=14$). Body (Fig. 1D) pear-shaped, differing from Nauplius III as follows: caudal margin with pair of minute spines representing Anlagen of caudal setae. Posterior end of body trilobate and becoming elongated.

Antennule (Fig. 2D) with a longer row of dentiform spinules distally on first segment. Third segment with 2 additional naked setae, plus extra row of long spinules midway along lateral margin.

Coxa of antenna (Fig. 3D) with spinular row midway along outer margin. Basis with 4 setae along inner margin; outer margin with 2 spinular rows on anterior surface and 1 spinular row on posterior surface. Apical segment of exopod with spinular row distally.

Basis of mandible with few mid-anterior surface spinules. Fourth segment of exopod with additional small seta distally (Fig. 4D).

Maxillule (Fig. 1D) bilobed with 2 spinulose and 1 naked seta on inner lobe. Outer lobe with 1 spinulose, 1 plumose and 1 long naked seta.

Nauplius V

Body length : mean \pm standard deviation = $210 \pm 8.49 \mu\text{m}$ (range 194 to 226 μm , $n=14$), mean body width $138 \pm 12.08 \mu\text{m}$ (range 122 to 157 μm , $n=14$). Body (Fig. 1E) similar to nauplius IV, differing as follows: third pair of caudal setae larger.

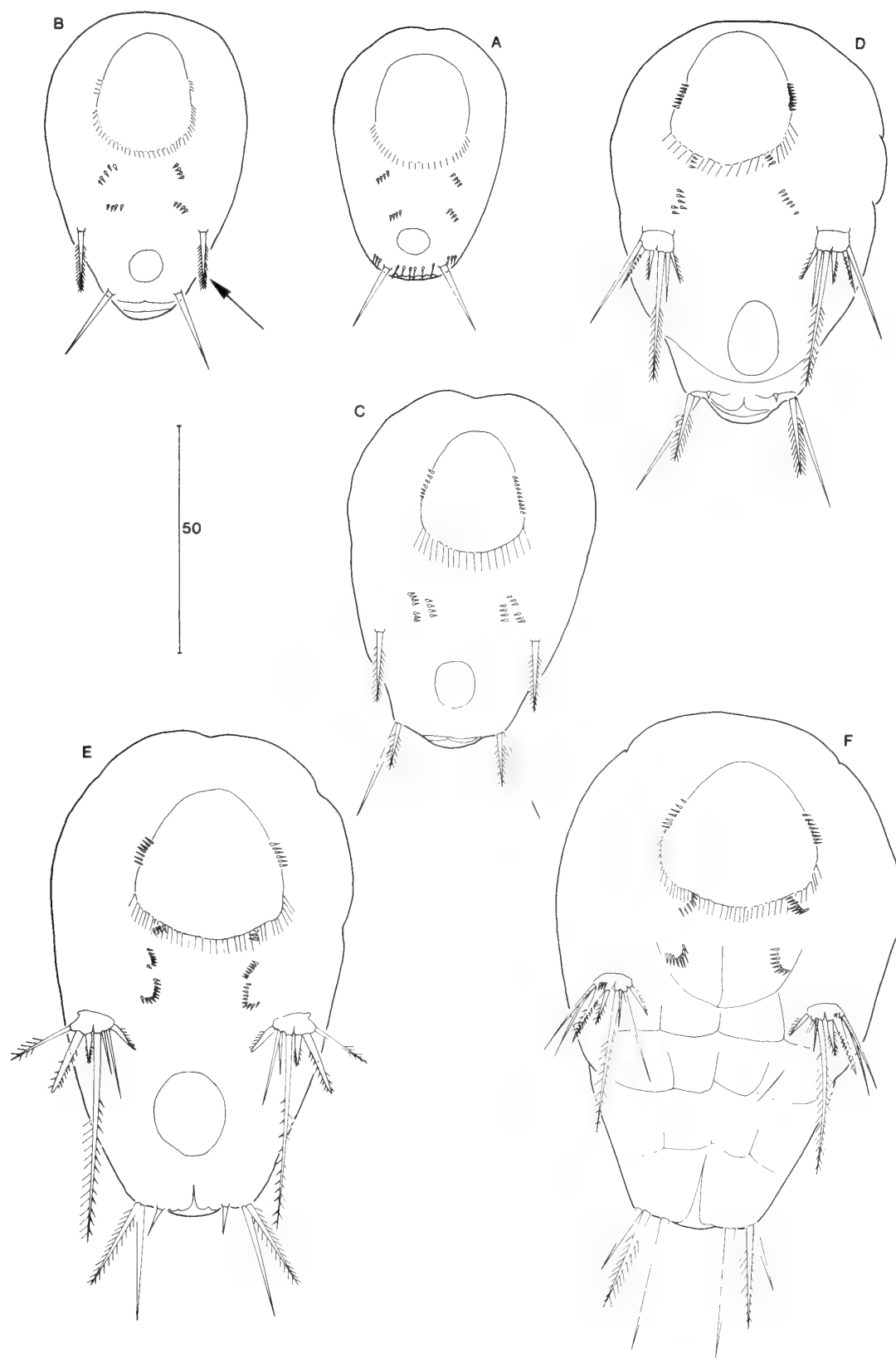


Fig. 1 *P. fimbriatus*. Naupliar stages, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Antennules, antennae and mandibles omitted. Scale bar in μm .

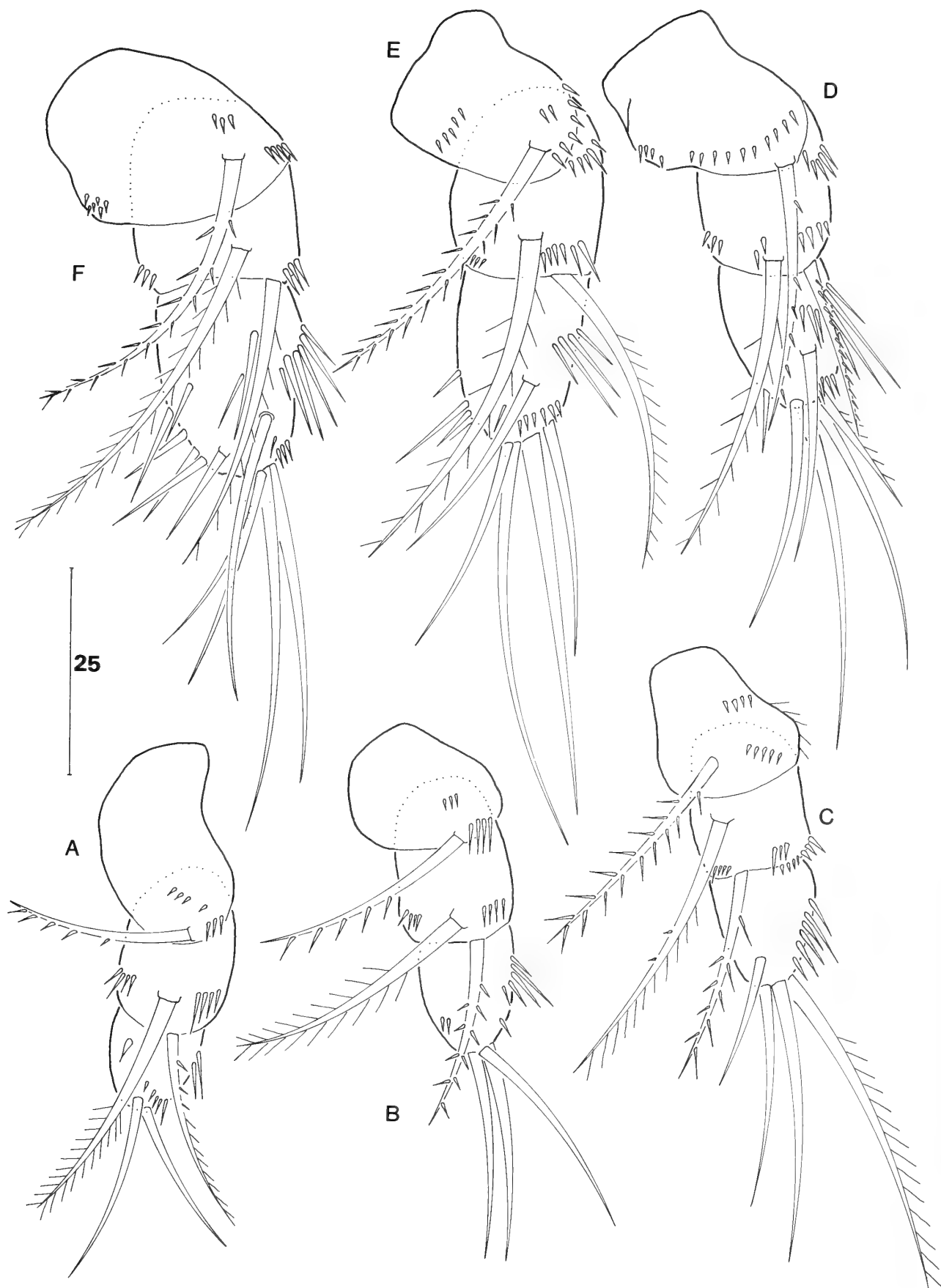


Fig. 2 *P. fimbriatus*. Naupliar antennules, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Scale bar in μm .

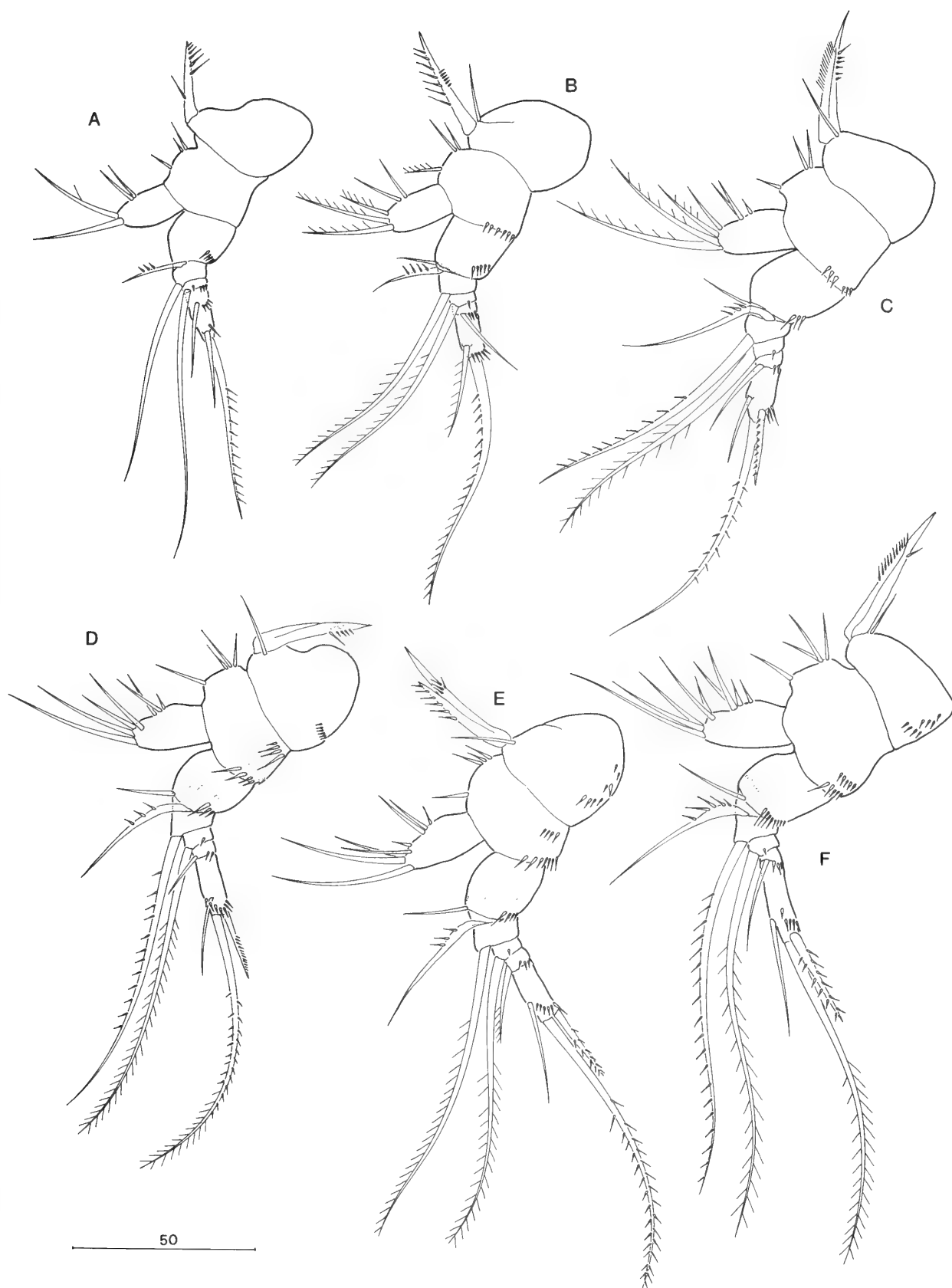


Fig. 3 *P. fimbriatus*. Naupliar antennae, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Scale bar in μm .

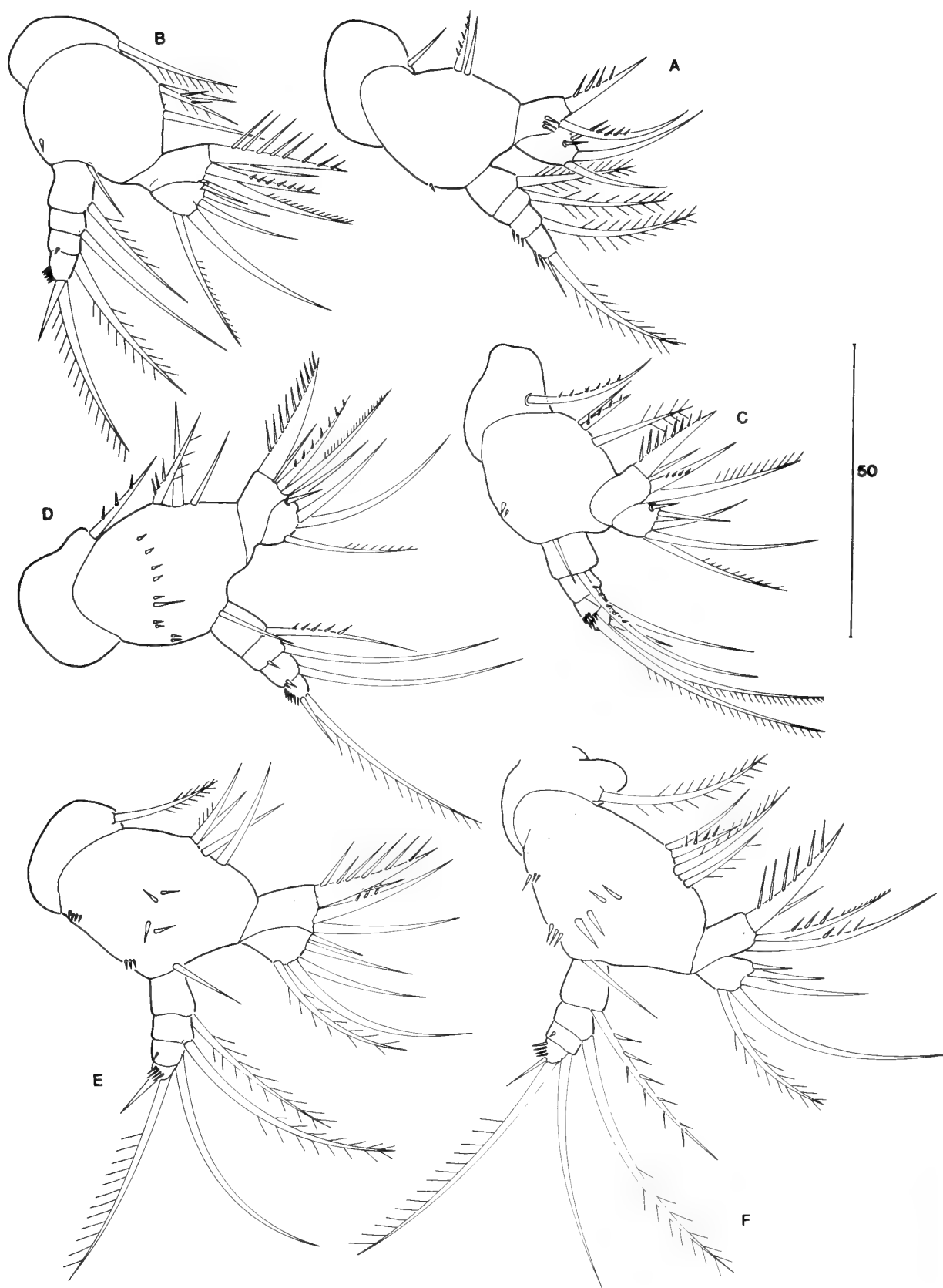


Fig. 4 *P. fimbriatus*. Naupliar mandibles, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Scale bar in μm .

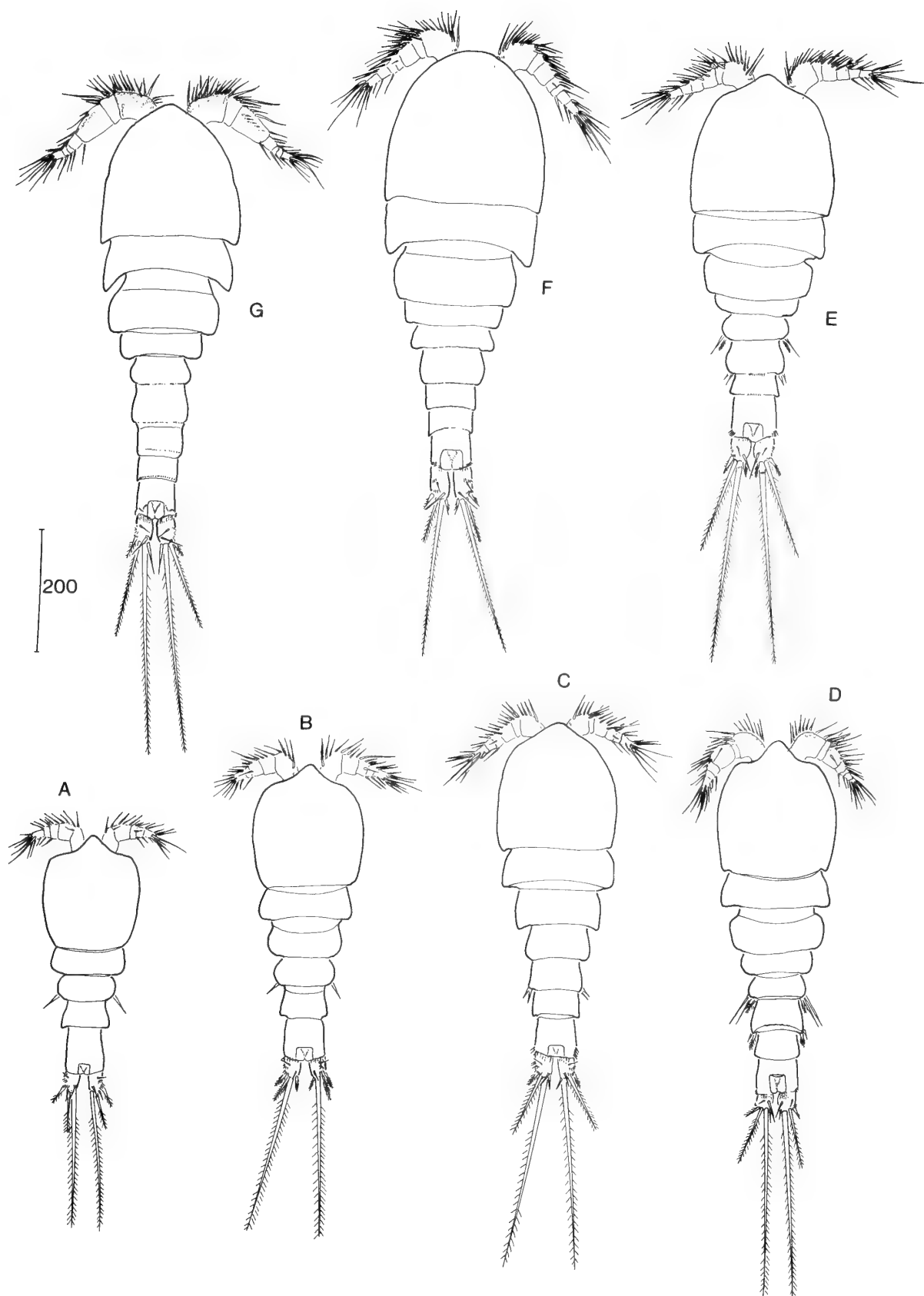


Fig. 5 *P. fimbriatus*. Dorsal view of Copepodid stages I–V. A, Female copepodid I; B, Female copepodid II; C, Female copepodid III; D, Male copepodid IV; E, Female copepodid IV; F, Female copepodid V; G, Male copepodid V. Scale bar in μm .

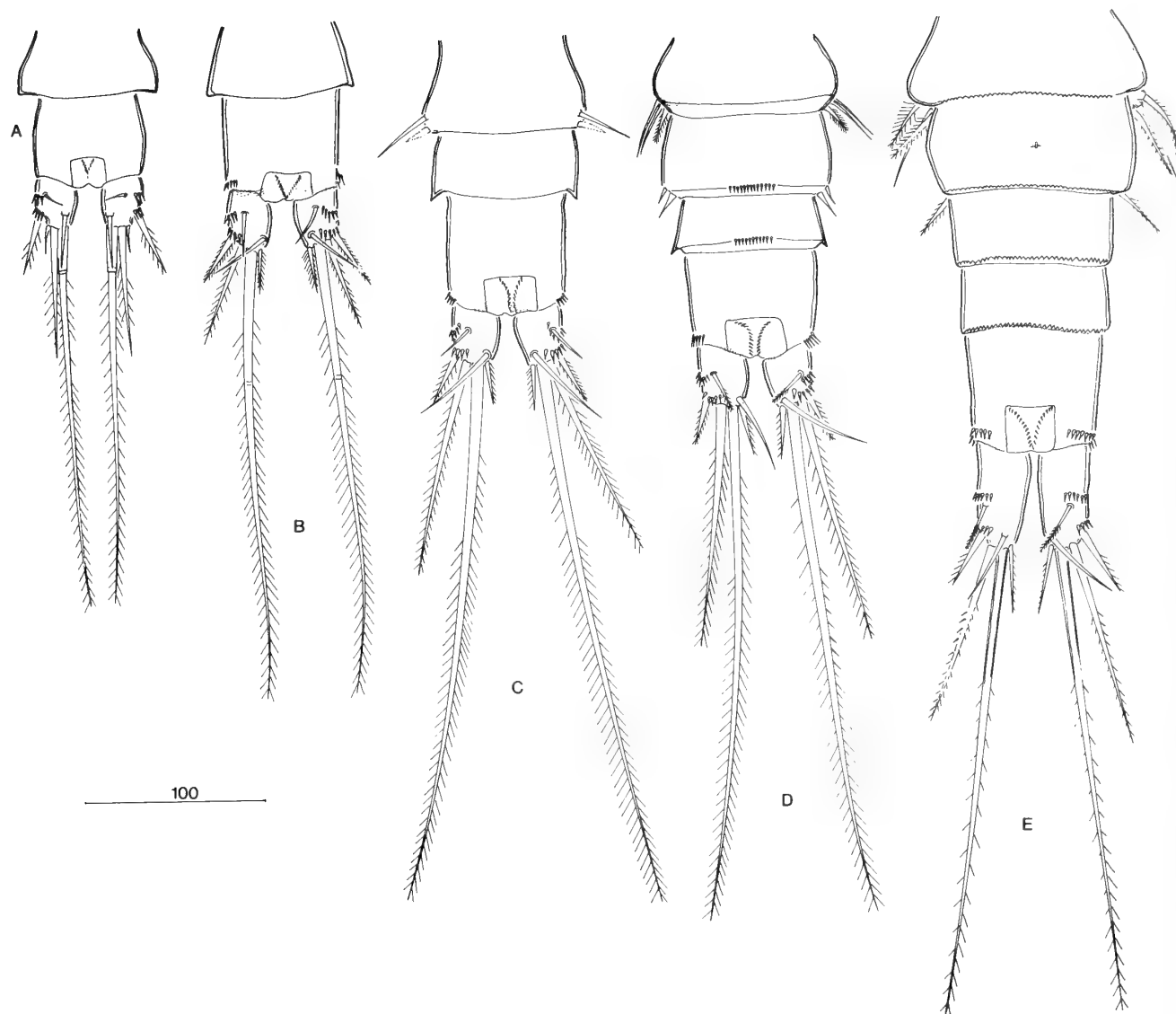


Fig. 6 *P. fimbriatus*. Urosome of female copepodids, dorsal. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V. Scale bar in μm .

First segment of antennule (Fig. 2E) with spinular row on outer margin. Third segment acquiring 3 small naked setae. Endopod of antenna (Fig. 3E) with additional small naked seta distally. Basis of mandible (Fig. 4E) with 4 setae. Maxillule (Fig. 1E) with 1 new naked seta on inner lobe.

Nauplius VI

Body length : mean \pm standard deviation = $241 \pm 8.49 \mu\text{m}$ (range 255 to 224 μm , $n=16$), mean body width 152 ± 7.28 (range 143 to 162 μm). Body (Fig. 1F) similar to nauplius V, differing as follows: innermost pair of caudal setae longest, middle pair of setae plumose, shortest setae naked and laterally located.

Third segment of antennule (Fig. 2F) with total of 13 setae, including 5 new setae, plus ornamentation of several long spinules. Endopod of antenna with 9 setae (Fig. 3F), with 1 extra seta in proximal group. Mandible (Fig. 4F) with minor changes in ornamentation of basal setae.

Maxillule with 1 new seta on inner lobe, and with 3 spinules on outer margin. Anlagen of post-maxillary limb pairs apparent on ventral surface of body (Fig. 1F).

Description of Copepodid Stages

Copepodid I

Body length : mean \pm standard deviation = $382 \pm 11.5 \mu\text{m}$ (range 373 to 404 μm , $n=10$), mean body width $146 \pm 5.7 \mu\text{m}$ (range 134 to 152 μm , $n=10$). Body 5-segmented (Fig. 5A), comprising cephalothorax and 4 postcephalothoracic trunk somites. Second trunk somite with 1 seta at posterolateral angles representing third swimming legs. Antennule, antenna, mandible, maxillule, maxilla, maxilliped and first and second swimming legs present. Caudal rami (Fig. 6A) as broad as long. Each ramus armed with 6 setae, ornamented with spinular row on ventral surface, outermost seta plumose with spinular row at base, 1 naked seta located on dorsal surface posteriorly, 1 short naked seta close to

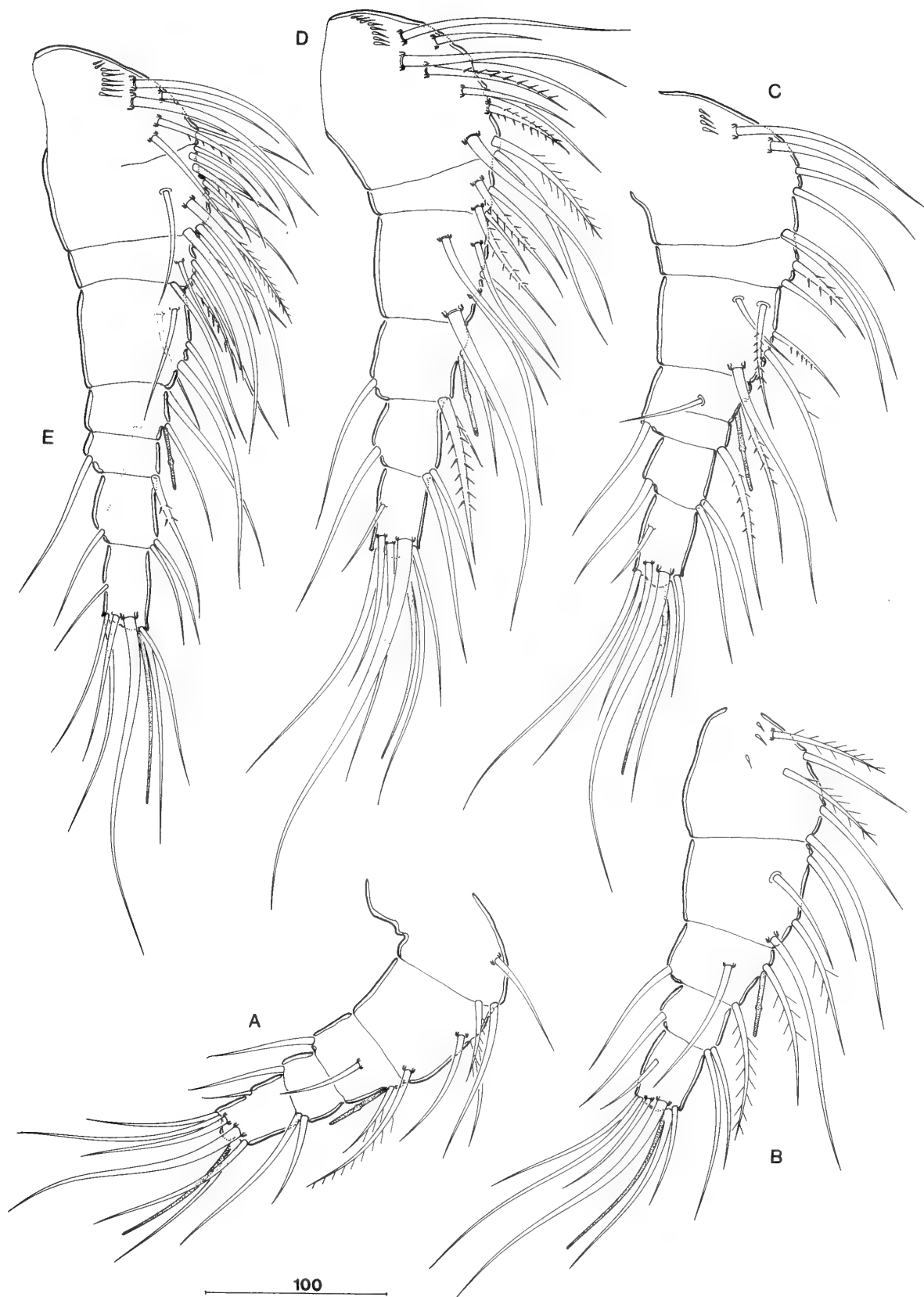


Fig. 7 *P. fimbriatus*. Development of female antennules. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V. Scale bar in μm.

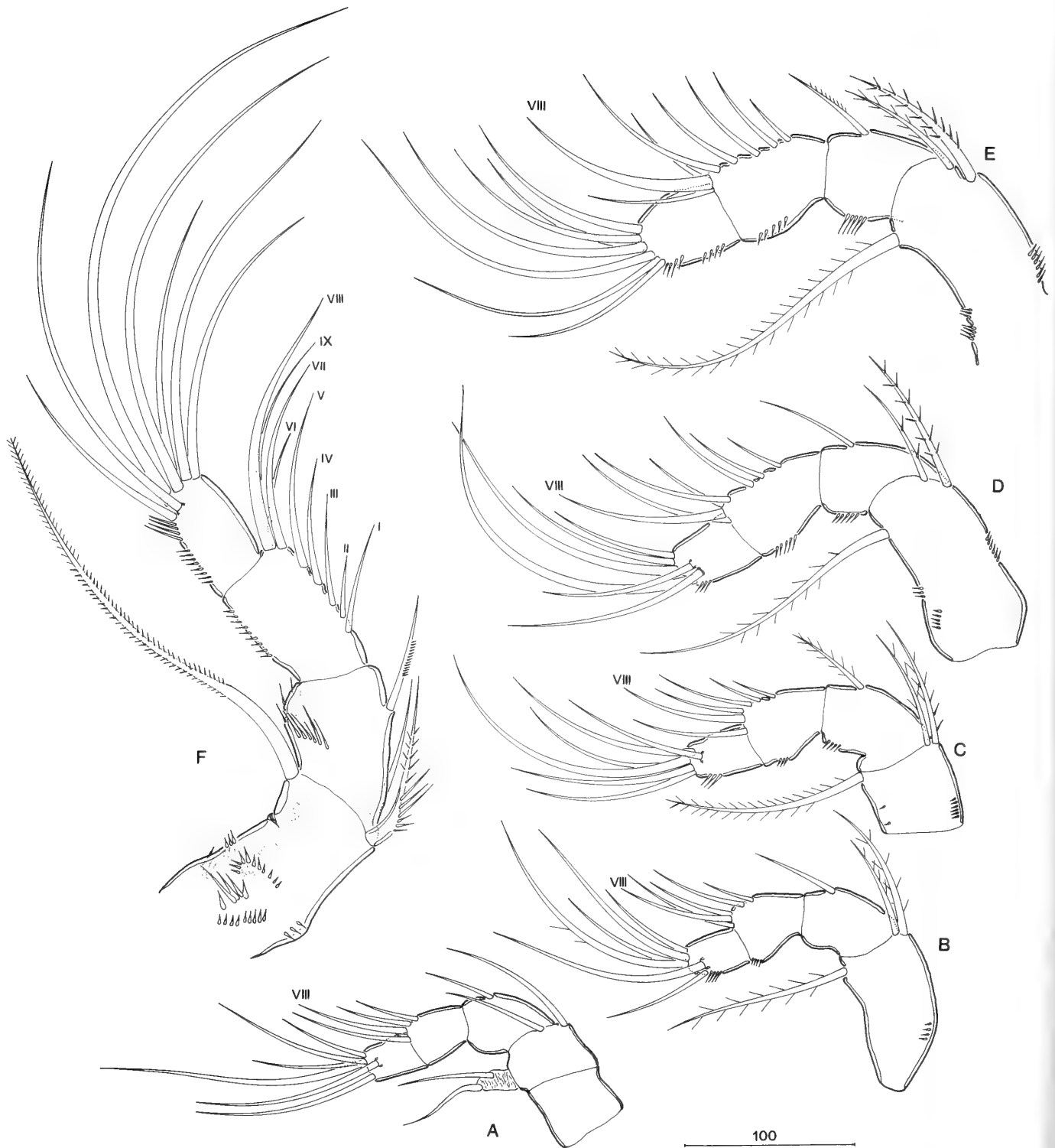


Fig. 8 *P. fimbriatus*. Development of copepodid antennae. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V; F, Copepodid VI. Scale bar in μm . [Setal numbering scheme of Boxshall & Evstigneeva (1994) is used.]

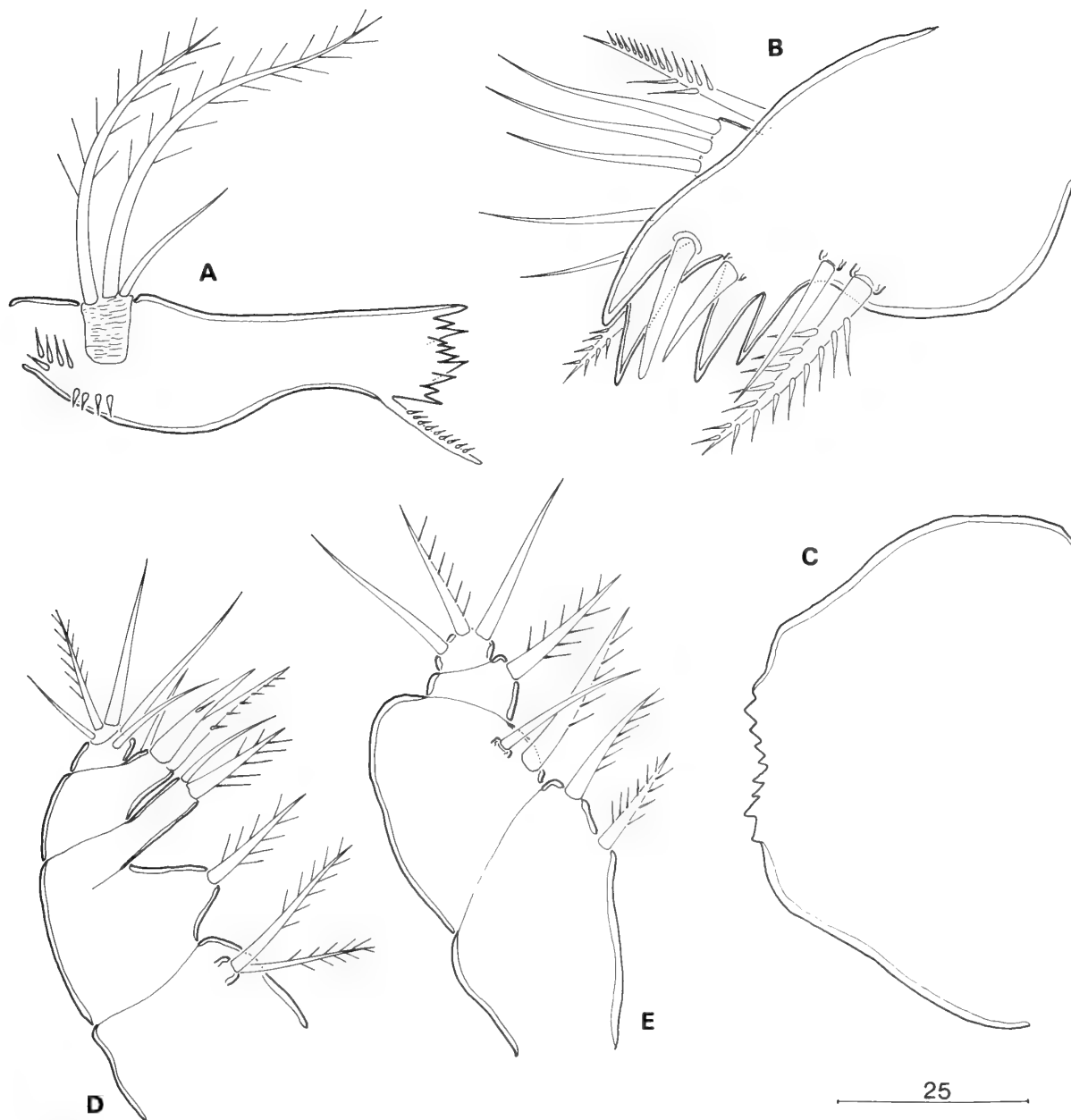


Fig. 9 *P. fimbriatus*. Copepodid I. A, Mandible, posteroventral; B, Maxillule, ventral; C, Labrum, ventral; D, Maxilla, anterior; E, Maxilliped, posterior. Scale bar in μm .

outermost seta, 2 inner plumose setae distally and 1 naked seta on dorsal outer margin. Anal operculum ornamented spinular row.

Antennule 5-segmented (Fig. 7A); aesthetasc at antero-distal angle of apical segment sharing common base with adjacent seta, as in all subsequent stages, including adult. Setal formula 3, 3, 3 + 1 aesthetasc, 3, 7 + 1 aesthetasc.

Antenna 5-segmented (Fig. 8A); coxa unarmed; basis with vestigial exopod bearing 2 naked setae, one apically and one halfway along inner margin. Basis armed with 2 inner angle setae. Endopod 3-segmented; setal formula 1, 4, 6. Labrum (Fig. 9C) with strong denticles along mid posterior margin.

Mandible (Fig. 9A) with well developed gnathobase bearing row of sharp blades medially, and 1 spinulose seta at inner distal angle. Vestigial mandibular palp with 2 long plumose setae and 1

naked seta distally. Inner posterior margin of mandible with two spinular rows.

Maxillule with strong praecoxa and reduced 2-segmented palp (Fig. 9B). Praecoxal endite armed with 4 setae articulating at base and 4 spines fused to segment. Proximal segment of palp derived from coxa and basis, bearing 2 naked and 1 spinulose inner margin setae, plus outer seta representing exopod. Distal segment of palp representing endopod, armed with 3 naked setae.

Maxilla (Fig. 9D) consisting of praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with single indistinct endite armed with 2 plumose setae. Coxa with inner seta at midlength and distal endite bearing strong plumose seta and naked seta apically. Basis with 3 setae distally. Endopod with 2 setae on proximal segment and 3 setae terminally.

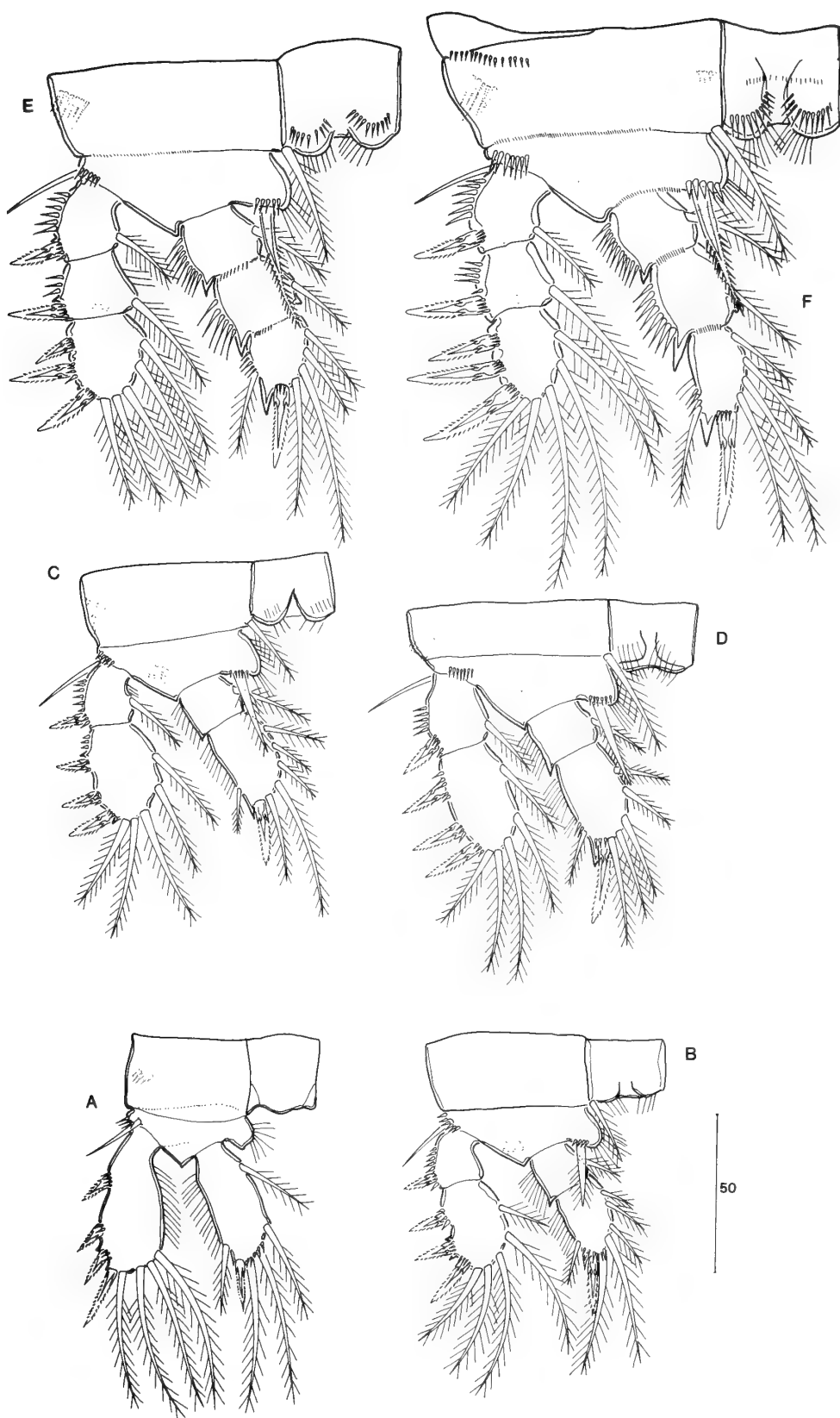


Fig. 10 *P. fimbriatus*. Leg I, anterior. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V; F, Copepodid VI (adult). Scale bars in μm .

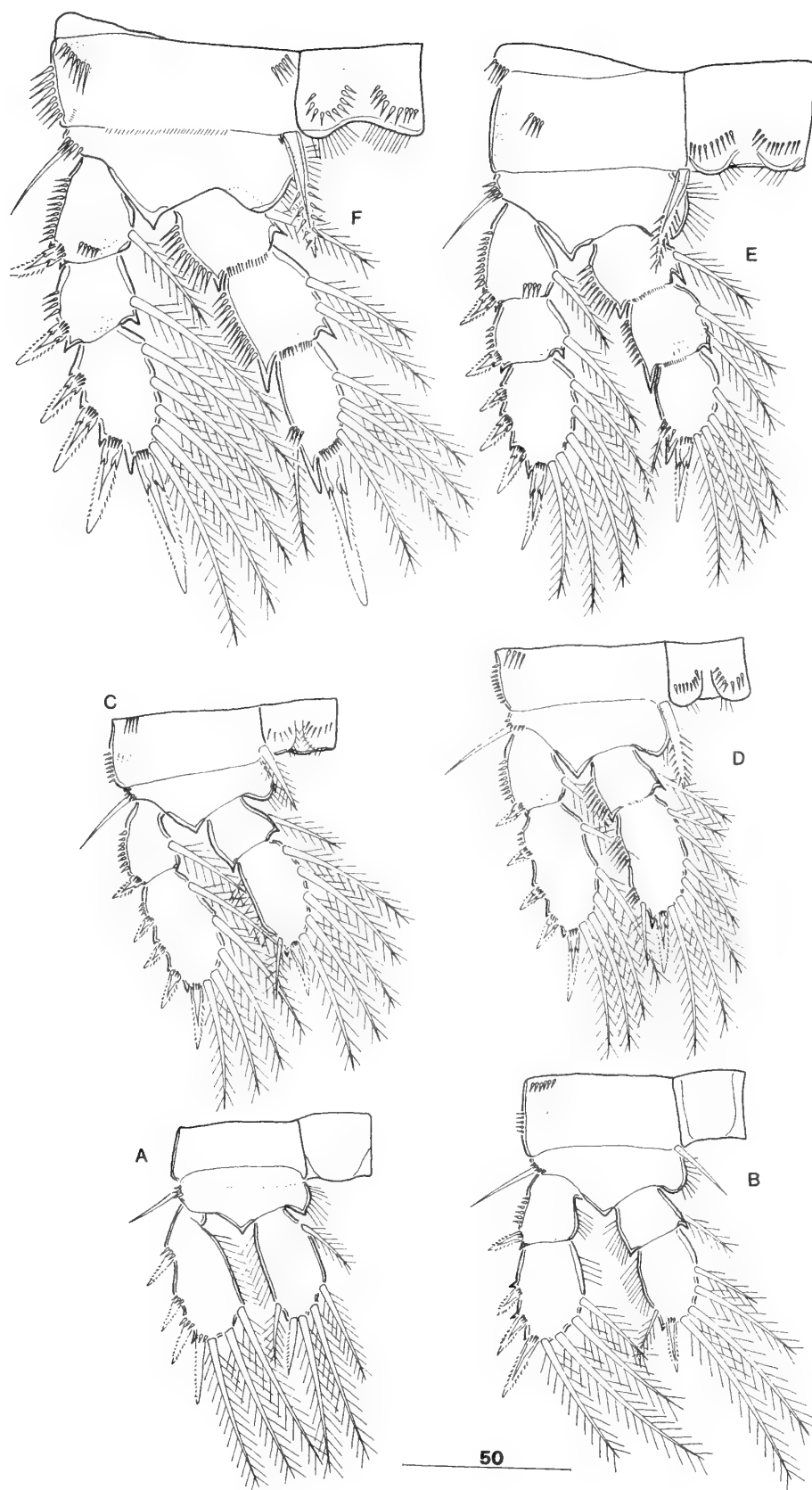


Fig. 11 *P. fimbriatus*. Leg 2, anterior. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V; F, Copepodid VI (adult). Scale bar in μm .

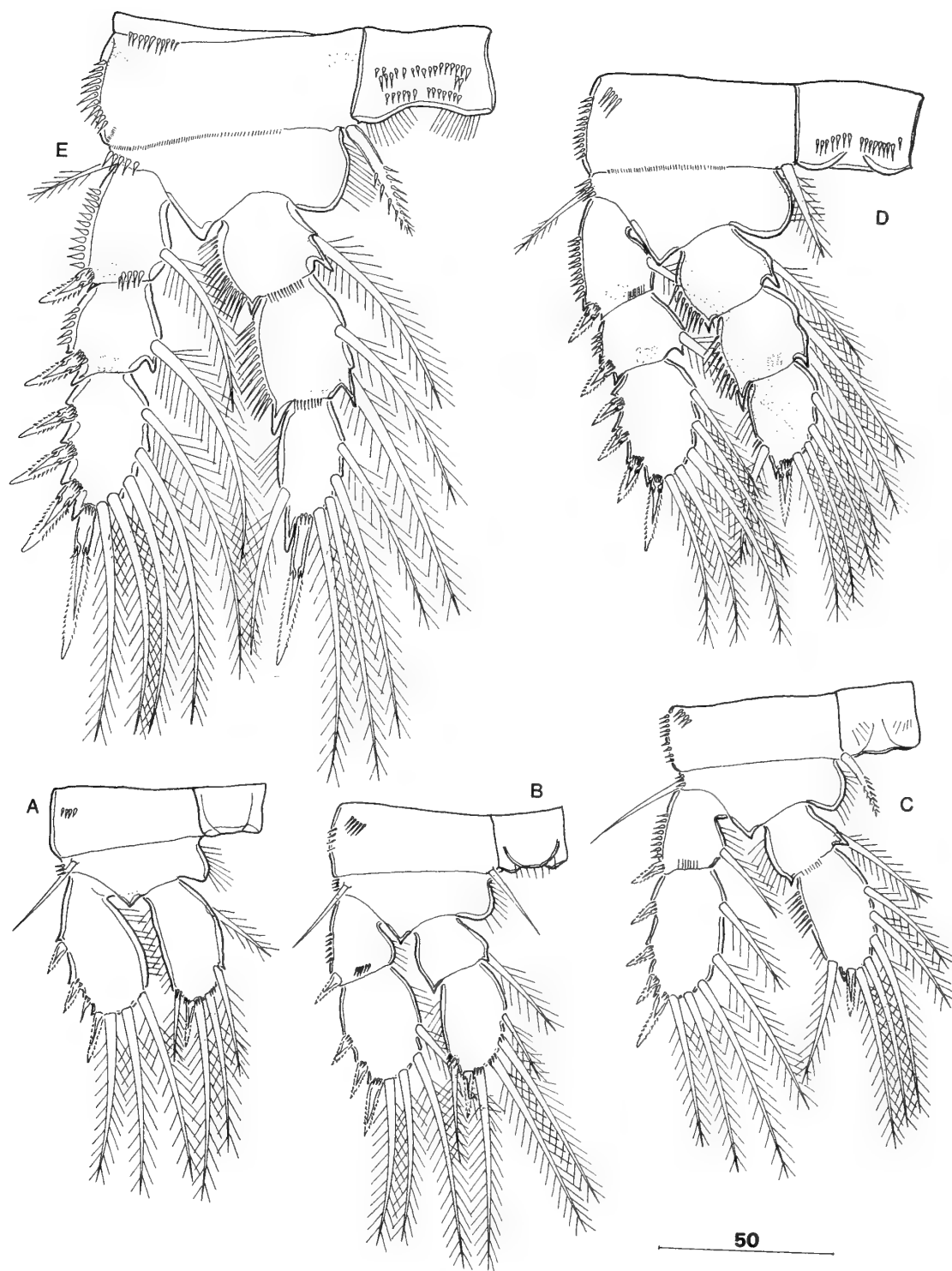


Fig. 12 *P. fimbriatus*. Leg 3, anterior. A, Copepodid II; B, Copepodid III; C, Copepodid IV; D, Copepodid V; E, Copepodid VI (adult). Scale bar in μm .

Maxilliped (Fig. 9E) distinctly 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa armed with 2 spinulose setae. Basis with 2 setae. Endopod segment 1 with 1 plumose seta; segment 2 with 3 setae.

Swimming legs 1 (Fig. 10A) and 2 (Fig. 11A) each with 2-segmented protopod. Intercoxal sclerites unornamented.

Coxa of leg 1 with spinular row posteriorly. Basis of both legs with outer angle seta ornamented by spinular row at base, inner basal margin with fine spinules. Both legs with 1-segmented rami. Inner margin of exopod and outer margin of endopod of both legs with row of pinnules. Spine and seta formula as follows:

| | Coxa | Basis | Exopod | Endopod |
|-------|------|-------|--------|---------|
| Leg 1 | 0-0 | 1-0 | IV,4 | 1,I+1,3 |
| Leg 2 | 0-0 | 1-0 | IV,3 | 1,I+1,3 |

Copepodid II

Body length : mean \pm standard deviation = $455 \pm 17.2 \mu\text{m}$ (range 439 to $488 \mu\text{m}$, $n=10$), mean body width $168 \pm 9.1 \mu\text{m}$ (range 152 to $178 \mu\text{m}$, $n=10$). Differing from Copepodid I as follows: body (Fig. 5B) 6-segmented, comprising cephalothorax and 5 postcephalothoracic trunk somites. Third trunk somite with 1 seta on outer margin representing fourth swimming legs. Last somite with posterior margin spinular rows ventrally and laterally (Fig. 6B).

Antennule with 3 spinules on first segment. Setal formula; 5, 4, 4 + 1 aesthetasc, 3, 7 + 1 aesthetasc (Fig. 7B).

Antenna 4-segmented (Fig. 8B); basis with spinular row near inner margin. Inner setae set close together at distal angle. Vestigial exopod represented by spinulose seta. First endopodal segment with 1 seta, second with 5 setae along distal margin and bearing small spinular row on outer margin. Third endopodal segment with 6 setae distally, ornamented with spinular row on outer distal margin.

Coxa of leg 1 with spinulose seta at inner distal angle (Fig. 10B). Basis with spinulose seta on inner distal margin ornamented with spinular rows at base of inner seta and posteriorly, between exopod and endopod. Intercoxal sclerite ornamented with setules distally. First segment of exopod with spinular row along outer margin. First and second segments of endopod with pinnules along lateral margins.

Coxa of leg 2 (Fig. 11B) with naked seta on inner distal margin; ornamented with spinular rows proximally on outer margin of both anterior and posterior surfaces and along outer margin. First segment of exopod with spinular rows laterally and proximally on posterior surface. Exopodal and endopodal segments with pinnules along inner and outer margins respectively.

Third leg (Fig. 12A) with 2-segmented protopod; coxa with spinular row proximally near outer margin. Basis with naked outer seta; ornamented with tiny spinules at base and hairs along inner margin. Intercoxal sclerite unornamented. Exopod and endopod 1-segmented, bearing pinnules along inner and outer margins respectively. Spine and seta formula as follows:

| | Coxa | Basis | Exopod | Endopod |
|-------|------|-------|------------|--------------|
| Leg 1 | 0-1 | 1-1 | I-0; III,5 | 0-1; 1,I+1,4 |
| Leg 2 | 0-1 | 1-0 | I-0; III,4 | 0-1; 1,I+1,3 |
| Leg 3 | 0-0 | 1-0 | IV,3 | 1,I+1,3 |

Copepodid III

Body length : mean \pm standard deviation = $511 \pm 22.8 \mu\text{m}$ (range 478 to $534 \mu\text{m}$, $n=10$), mean body width $179 \pm 5.3 \mu\text{m}$ (range 173 to $186 \mu\text{m}$, $n=10$). Differing from copepodid II as follows: body (Fig. 5C) 7-segmented, comprising 4-segmented prosome bearing swimming legs 1 to 4, and 3-segmented urosome (Fig. 6C).

Antennule 6-segmented (Fig. 7C): fourth segment partly divided. Setal formula: 6, 2, 5, 4 + 1 aesthetasc, 3, 7 + 1

aesthetasc. Antenna (Fig. 8C) with spinular row on inner margin of second segment proximally. Second endopodal segment with 6 setae. Labrum with long spinular rows along lateral margins distally.

Exopod of legs 1 (Fig. 10C) and 2 (Fig. 11C) with new seta on inner margin of first segment. Intercoxal sclerite of leg 2 ornamented with rows of setules on anterior surface. Second endopodal and exopodal segments each with new seta. Coxa of third leg (Fig. 12B) with new seta at inner angle and bearing spinular row on outer margin. Intercoxal sclerite ornamented. Exopod and endopod 2-segmented. Leg 4 (Fig. 13A) with 2-segmented protopod; coxa with spinular row on outer margin. Basis with outer angle seta and bearing spinular row on laterally. Exopod and endopod 1-segmented. Intercoxal sclerite unornamented. Leg 5 (Fig. 6C) represented by 2 setae. Spine and seta formula as follows:

| | Coxa | Basis | Exopod | Endopod |
|-------|------|-------|------------|--------------|
| Leg 1 | 0-1 | 1-1 | I-1; III,5 | 0-1; 1,I+1,4 |
| Leg 2 | 0-1 | 1-0 | I-1; IV,5 | 0-1; 1,I+1,4 |
| Leg 3 | 0-1 | 1-0 | I-0; III,4 | 0-1, 1,I+1,3 |
| Leg 4 | 0-0 | 1-0 | IV,3 | 1,I+1,3 |

Female copepodid IV

Body length : mean \pm standard deviation = $573 \pm 19.5 \mu\text{m}$ (range 547 to $608 \mu\text{m}$, $n=10$), mean body width $200 \pm 14 \mu\text{m}$ (range 178 to $221 \mu\text{m}$, $n=10$). Differing from copepodid III as follows: body (Fig. 5E) 8-segmented with 4-segmented urosome (Fig. 6D); spinular rows present mid-dorsally along posterior margins of urosomites 2 and 3.

Antennule 6-segmented (Fig. 7D) with entire fourth segment. Setal formula; 11, 4, 5, 4 + 1 aesthetasc, 3, 7 + 1 aesthetasc. Antenna with 2 short spinular rows dorsally on inner side of first segment. Second endopodal segment with 7 setae (Fig. 8D). Mandible with spinular row on ventral margin of coxa. Maxilliped with spinular rows midway along outer margin and on anterior surface near inner setae.

Legs 1-4 with 2-segmented rami (Figs 10D, 11D, 12C, 13B). Coxa of leg 4 with naked seta at inner angle proximally and spinular row on outer margin. Spine and seta formula as follows:

| | Coxa | Basis | Exopod | Endopod |
|-------|------|-------|------------|--------------|
| Leg 1 | 0-1 | 1-1 | I-1; III,5 | 0-1; 1,I+1,4 |
| Leg 2 | 0-1 | 1-0 | I-1; IV,5 | 0-1; 1,I+1,5 |
| Leg 3 | 0-1 | 1-0 | I-1; IV,5 | 0-1; 1,I+1,4 |
| Leg 4 | 0-1 | 1-0 | I-0; IV,5 | 0-1; 1,II,3 |

Leg 5 with 3 setae; leg 6 represented by 2 simple setae at posterolateral angle of second urosomite (Fig. 6D)

Male copepodid IV

Body length, (range 565 to $643 \mu\text{m}$, $n=2$), body width, (range 195 to $204 \mu\text{m}$, $n=2$). Differing from female Copepodid IV as follows: anterior part of body (Fig. 5D) not much broader than posterior compared with female; constriction between somites bearing 4th and 5th legs (Fig. 14A) not as distinct.

Appendages as in female fourth copepodid except as follows: antennule 6-segmented (Fig. 15A) but segment 3 broader. Segments 3 and 4 with distinctive short spiniform setation

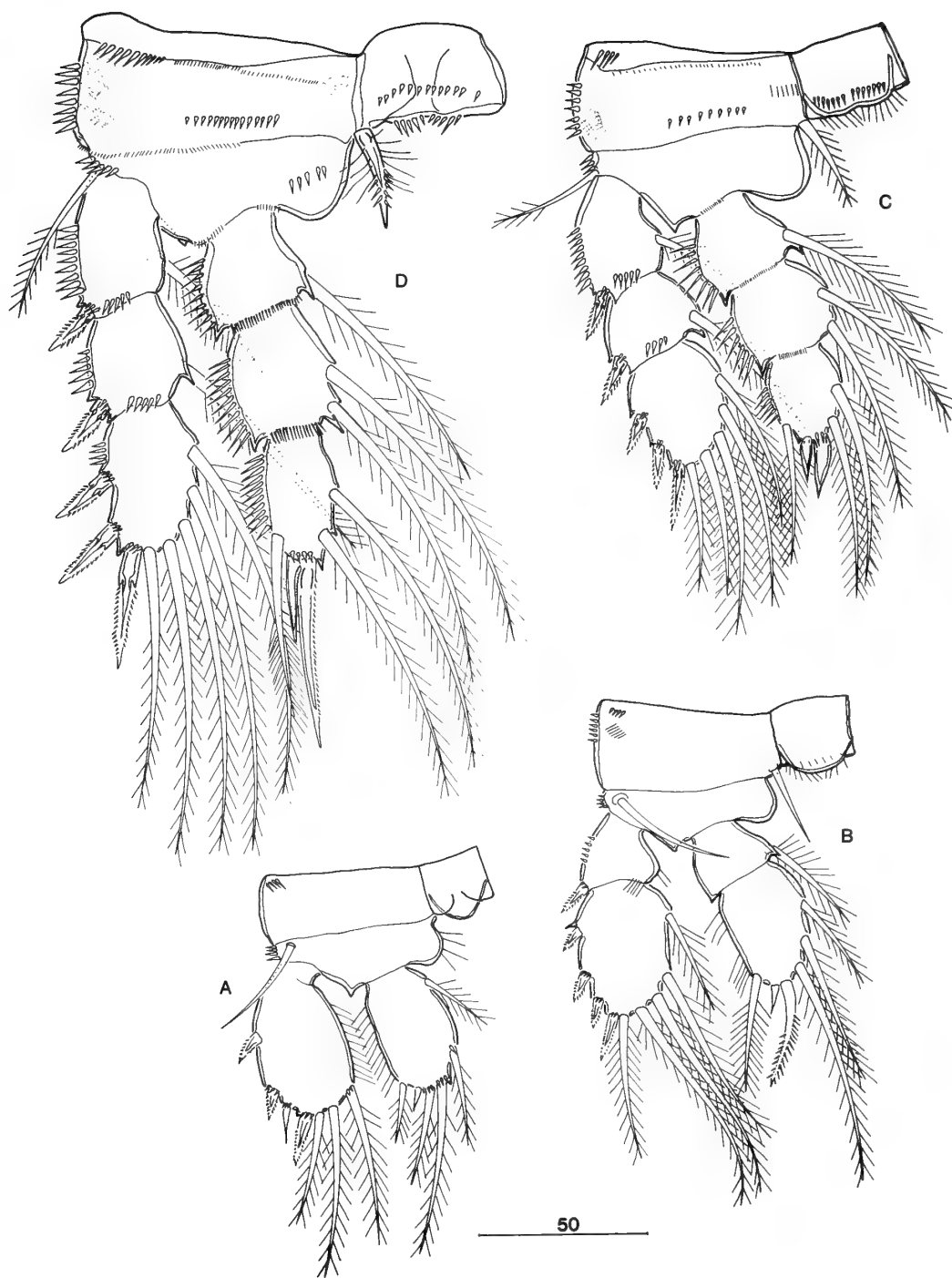


Fig. 13 *P. fimbriatus*. Leg 4, anterior. A, Copepodid III; B, Copepodid IV; C, Copepodid V; D, Copepodid VI (adult). Scale bar in μm .

elements (arrowed in Fig. 16D). Setal formula: 11, 4, 5 + spine, 4 + spine + 1 aesthetasc, 3, 7 + 1 aesthetasc.

Female copepodid V

Body length : mean \pm standard deviation = $726 \pm 38.47 \mu\text{m}$ (range 647 to $769 \mu\text{m}$, $n=10$), mean body width $246 \pm 12.4 \mu\text{m}$

(range 217 to $260 \mu\text{m}$, $n=10$). Differing from female Copepodid IV as follows: body 9-segmented (Fig. 5F) with 5-segmented urosome (Fig. 6E); anal somite with dense spinular row along posterior margin extending from ventral surface to dorsal margin, either side of anal slit. Caudal rami about 3 times as long as broad.

Antennule 7-segmented (Fig. 7E) : setal formula; 18, 6, 5, 2 + 1

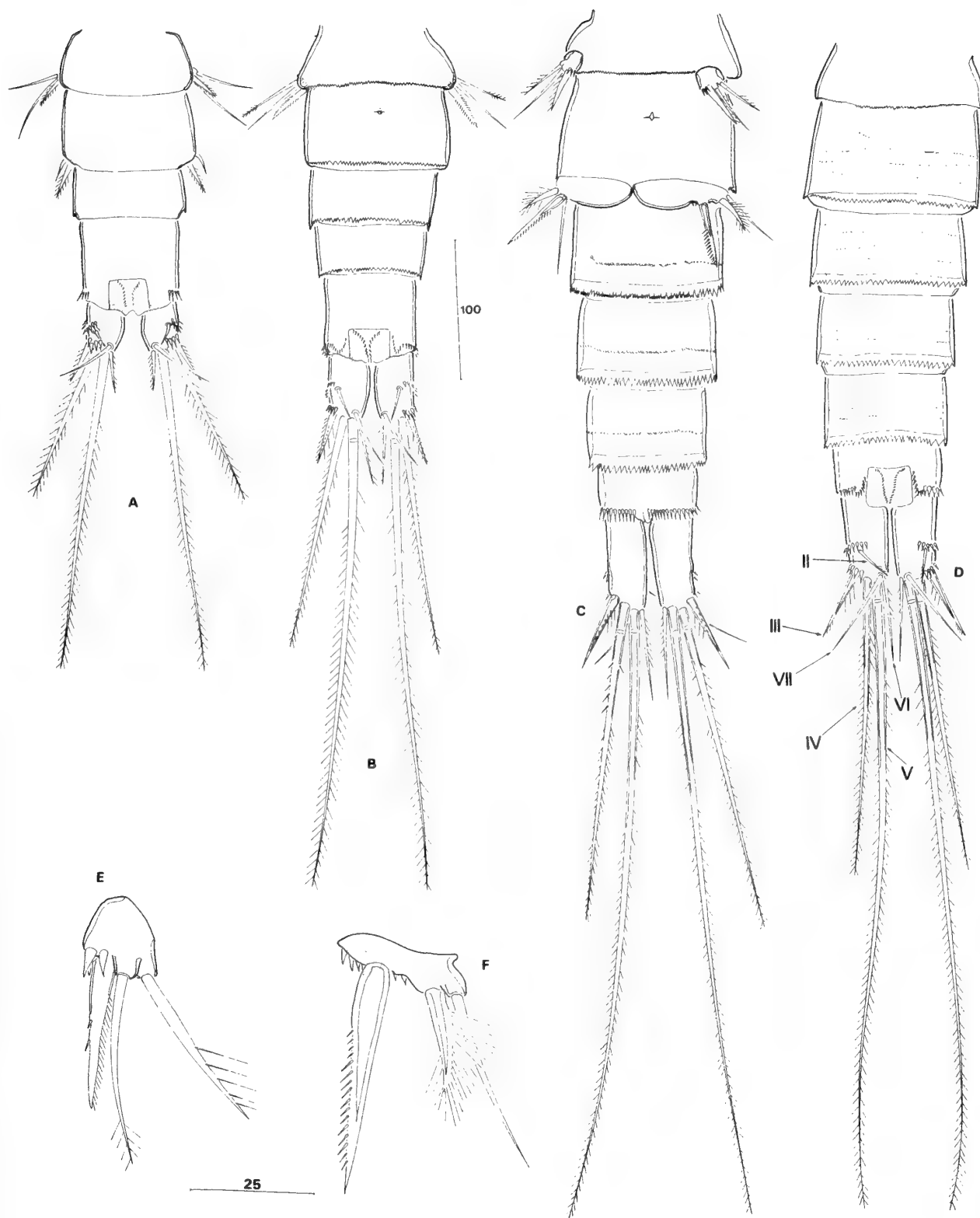


Fig. 14 *P. fimbriatus*. Male. A, Copepodid IV urosome, dorsal; B, Copepodid V, dorsal; C, adult urosome, ventral; D, adult urosome, dorsal; E, Adult leg 5, ventral; F, Adult leg 6, ventral. Scale bars in μm .



Fig. 15 *P. fimbriatus*. Male antennules, lateral. A, Copepodid IV; B, Copepodid V. Scale bar in μm .

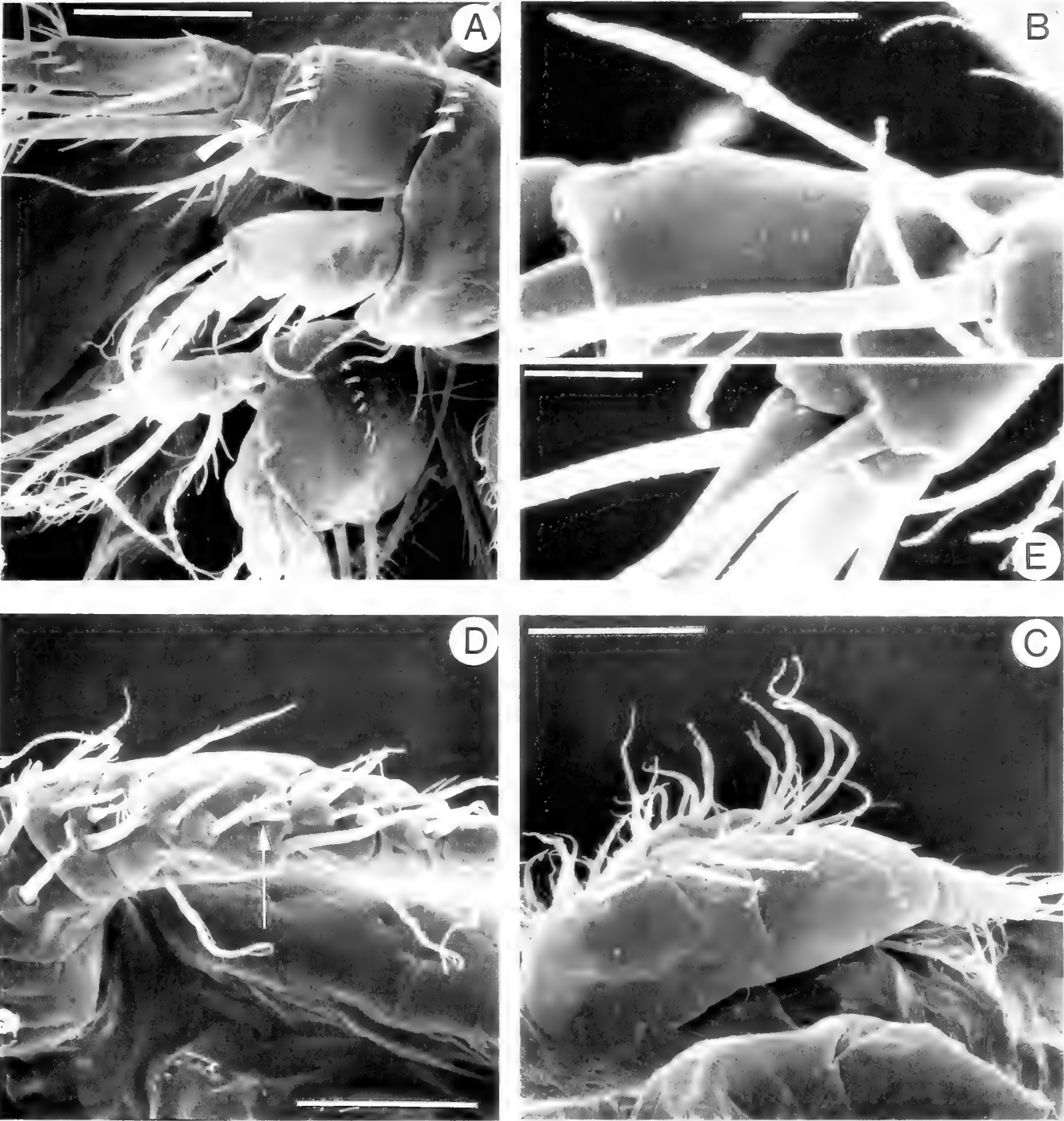


Fig. 16 Scanning electron micrographs of *P. fimbriatus*. A, Nauplius VI antenna, ventral; arrow indicates minute second exopodal segment; B, Adult female antennule, aesthetasc on segment 5; C, Male copepodid V antennule, dorsal; D, Male copepodid IV antennule, ventral; arrow indicates the spine on segment 4; E, Adult female antennule, double fusion on terminal segment, lateral. Scale bars A = 20 μ m, B = 5 μ m, C = 40 μ m, D = 25 μ m, E = 5 μ m.

aesthetasc, 2, 3, 7 + 1 aesthetasc. Second endopodal segment of antenna (Fig. 8E) with 8 setae; distal seta VIII stronger than others. Praecoxal arthrite of maxillule with 5 setae. Proximal spinulose seta ornamented with long spinules. Praecoxa of maxilla with short spinular row on outer margin. Basis of maxilliped with 2 spinular rows laterally.

Leg 1 (Fig. 10E) with 3-segmented exopod and endopod, bearing spinular row posteriorly on second segment of exopod. Intercoxal sclerite with anterior spinular rows distally. Leg 2 (Fig. 11E) with praecoxa bearing spinular row on outer margin. Exopod and endopod 3-segmented: first segment of exopod with proximal spinular row anteriorly, second exopodal and

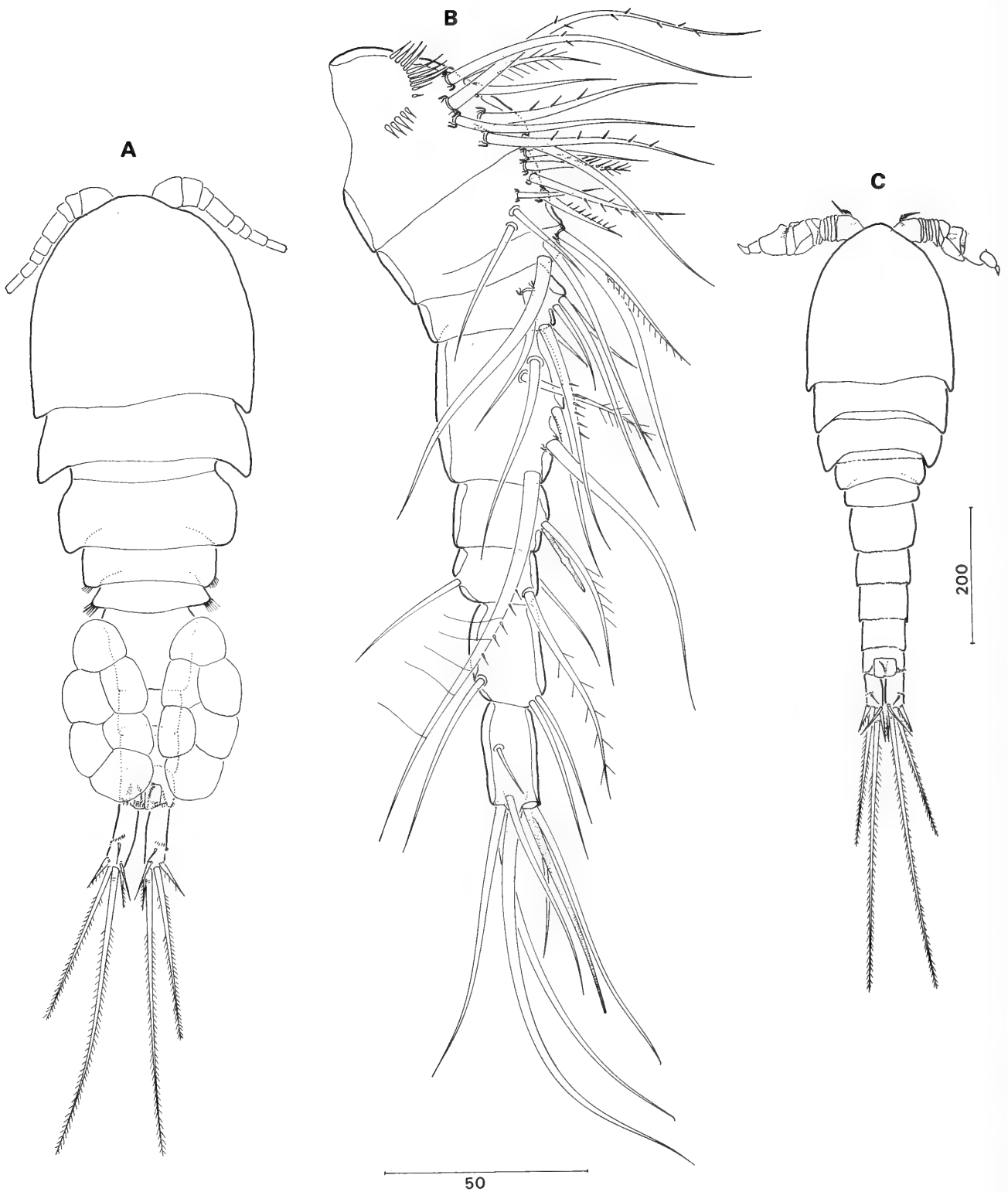


Fig. 17 *P. fimbriatus*. A, Adult female, dorsal; B, Adult female antennule, dorsal; C, Adult male, dorsal. Scale bars in μm .

endopodal segments with spinular rows posteriorly. Leg 3 (Fig. 12D) with 3-segmented exopod and endopod bearing posterior spinular rows on first and second segments of exopod and second segment of endopod. Intercoxal sclerite with transverse spinular row on anterior surface. Leg 4 (Fig. 13C) with praecoxa bearing spinular row on outer margin. Coxa with posterior

spinular row near outer proximal angle, spinular row on midanterior surface and very fine spinules along posterior margin. Exopod and endopod 3-segmented: first and second segments of exopod with anterior spinular rows distally. Intercoxal sclerite with transverse spinular row on anterior surface. Spine and seta formula as follows:

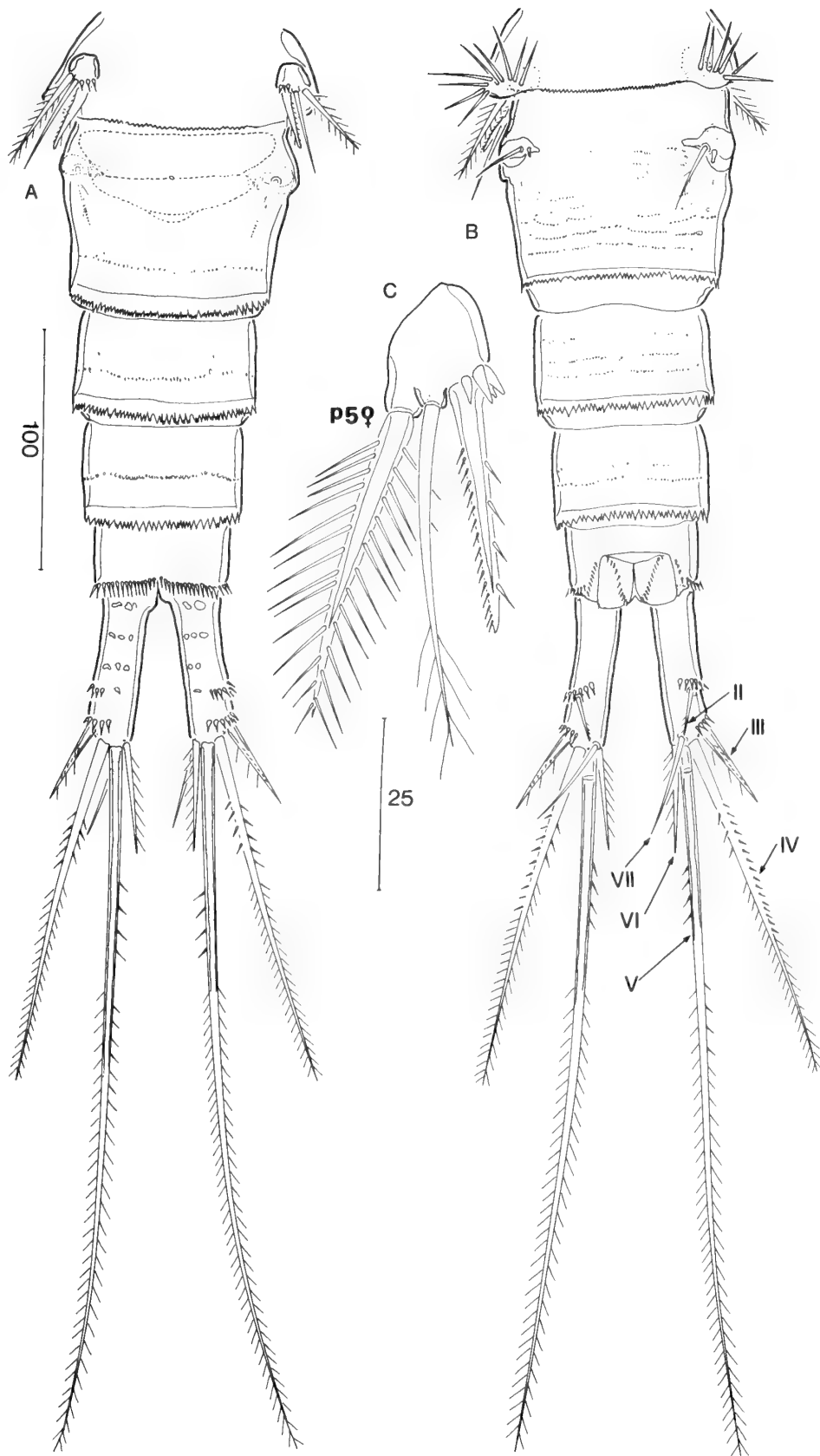


Fig. 18 *P. fimbriatus*. Adult female. A, urosome, ventral; B, urosome, dorsal. C, leg 5, ventral. Scale bars in μm .

| | Coxa | Basis | Exopod | Endopod |
|-------|------|-------|-----------------|----------------|
| Leg 1 | 0-1 | 1-1 | 1-1;1-1;III,1,4 | 0-1;0-1;1,1,4 |
| Leg 2 | 0-1 | 1-0 | 1-1;1-1;III,1,5 | 0-1;0-2;1,1,4 |
| Leg 3 | 0-1 | 1-0 | 1-1;1-1;III,1,5 | 0-1;0-2;1,1,4 |
| Leg 4 | 0-1 | 1-0 | 1-1;1-1;III,1,4 | 0-1;0-2;1,II,2 |

Leg 6 represented by 1 plumose and 1 naked seta at posterolateral angle of second urosomite (Fig. 6E)

Male Copepodid V

Mean body length: mean \pm standard deviation = $695 \pm 44.83 \mu\text{m}$ (range 634 to $743 \mu\text{m}$, $n=7$), mean body width $216 \pm 8.1 \mu\text{m}$ (range 200 to $221.73 \mu\text{m}$). Differing from male Copepodid IV as follows: body 9-segmented: first to fourth urosomites ornamented along posterior margins (Fig. 14B). Anal somite densely furnished with spinules along distal margin and extending either side of anal operculum.

Appendages as in fourth copepodid except as follows: antennule (Fig. 15B) 7-segmented; proximal 3 segments much enlarged, swollen (Figs 16C) first segment with one modified spiniform seta (stippled on Fig. 15B); segment 3 with 6 similarly modified elements and segment 4 with 1 such element. Setal formula; 19 + 1 spine, 5, 5 + 6 spines, 2 + 1 aesthetasc + 1 spine, 2, 3, 7 + 1 aesthetasc.

Leg 6 (Fig. 14B) represented by 3 setae, not visible in dorsal view.

Adult female

Body length: mean \pm standard deviation = $935 \pm 61.07 \mu\text{m}$ (range 833 to $1013 \mu\text{m}$, $n=10$), mean body width $307 \pm 14.9 \mu\text{m}$ (range 291 to $330 \mu\text{m}$, $n=10$). Body (Fig. 17A) comprising 4-segmented prosome and 5-segmented urosome. Prosome with cephalothorax and 3 free pedigerous somites decreasing in width from anterior to posterior. Cephalothorax narrowing anteriorly; widest approximately in middle. Third and fourth pedigerous somites with lateral groups of bristles at posterolateral angles. Urosome (Figs 18A,B) consisting of 5th pedigerous somite, genital double-somite and 3 free abdominal somites. Genital double-somite about as long as broad. Genital double-somite and first 2 free abdominal somites with surface ornamentation dorsally and ventrally: fifth pedigerous somite with ornamentation along posterior margin. Anal somite with spinular row ventrally extending round to anal operculum (Fig. 19A). Anal operculum smooth; row of spinules present in anal cleft either side of midline (Fig. 19D).

Caudal rami about 3.5 times longer than broad with ornamentation comprising rows of pits or cuticular depressions on ventral surface (Fig. 19B). Generally held wide apart, slightly divergent. Caudal rami with 6 setae; seta I missing; outer lateral seta (III) with spinular row at base extending dorsally and ventrally; small seta (II) on dorsolateral surface with spinular row behind it and extending ventrally.

Antennule 8-segmented (Fig. 17B), quite short. First segment with spinular row ventrally. Segment 2 with partial suture line. Fourth segment longest. Segment 5 distinctive with short aesthetasc (Fig. 16B); apical segment with aesthetasc fused to adjacent seta at base (Fig. 16E). Setal formula: 8, 12, 6, 5, 2 + 1 aesthetasc, 2, 3, 7 + 1 aesthetasc. One element on seventh segment possibly a setiform aesthetasc (see discussion below).

Antenna 4-segmented (Fig. 8F), comprising coxobasis and 3-segmented endopod. Coxobasis with complex ornamentation

as figured and armed with 2 inner setae, and 1 outer spinulose seta representing exopod. First endopodal segment with inner distal seta and midsurface spinular row. Second endopodal segment with 9 setae, of which 5 on inner margin and 4 arranged along inner part of distal margin; segment ornamented with spinules along outer margin. Third endopodal segment armed with 7 setae around apex; segment ornamented with spinular row along outer margin.

Labrum with complex ornamentation on ventral surface (Fig. 20A). Anterior part broader than posterior part. Posterior margin forming strong teeth.

Mandible (Fig. 20B) consisting of well developed coxal gnathobase and reduced palp. Gnathobasic blades mostly simple, dorsal seta with spinules along inner rim. Palp represented by 3 setae, one long and spinulose, the other plumose. Third seta short and naked. Central surface of coxa with 3 spinular rows and another spinular row on margin at base of gnathobase.

Maxillule (Fig. 20C) consisting of powerful praecoxa and reduced 2-segmented palp. Praecoxal arthrite armed with 7 setae articulating at base and 4 spines fused to segment; proximalmost seta spinulose, spines naked. Proximal segment of palp derived from coxa and basis, bearing 2 naked and 1 spinulose inner margin setae, plus outer seta representing exopod. Distal segment of palp, representing endopod, armed with 2 setae with spinules along margin and 1 naked seta.

Maxilla 5-segmented (Fig. 20D), comprising praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with spinular row on outer margin. Praecoxal endite with 2 setae, 1 of which spinulose. Coxa with proximal endite represented by single seta, distal endite with well developed process carrying strong spinulose seta and naked seta apically. Basis drawn out into powerful spinulate claw and armed with strong accessory claw with spinular row along convex margin and naked seta. First endopodal segment carrying 2 spinulose setae, second carrying 3 setae.

Maxilliped 4-segmented (Fig. 20E), comprising syncoxa, basis and 2-segmented endopod. Syncoxa armed with 3 inner margin setae representing endites; ornamented with spinular row near middle of inner margin and 2 spinules on outer margin. Basis armed with 2 inner setae, 1 of which with spinules; ornamented with 2 transverse rows of spinules near outer distal angle and another spinular row midway along outer margin. First endopodal segment bearing claw-like seta with 5 spinules at midlength. Second endopodal segment with 3 setae, 2 of which bearing spinules midway; outermost naked.

Legs 1 to 4 each with complex ornamentation on anterior and posterior surfaces of coxa as figured; also ornamented on intercoxal sclerite. Legs 1 to 3 with spinular rows on posterior surface of exopodal segments 1 and 2, and endopodal segment 2.

Leg 1 (Fig. 10F) with 3-segmented protopod. Praecoxa represented by triangular sclerite at outer proximal angle. Coxa with inner plumose seta. Basis with outer angle seta and setiform spine on inner margin; bearing spinular row on posterior surface. Both seta and spine with spinular rows at bases.

Legs 2 (Fig. 11F) and 3 (Fig. 12E) with 3-segmented protopods. Coxa with inner setiform spine. Outer seta on basis with spinular row at base. First segment of exopod with spinular row on anterior surface.

Leg 4 (Fig. 13D) with 3-segmented protopod. Praecoxa represented by thin, hooped sclerite. Coxa with inner setiform spine. Basis with outer seta bearing spinular row at base; spinular row on inner margin anteriorly. Segments 1 and 2 of

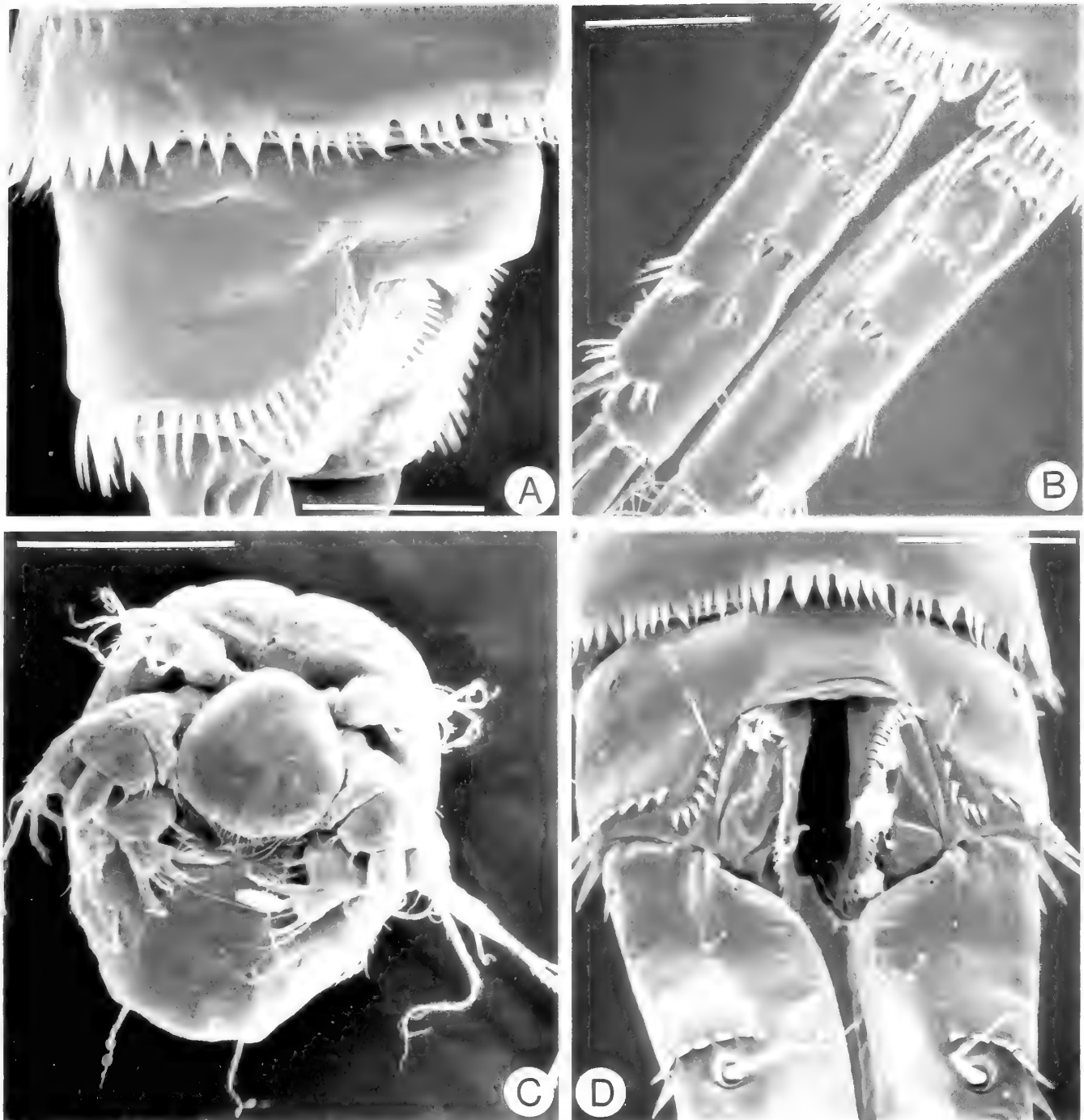


Fig. 19 Scanning electron micrographs of *P. fimbriatus*. A, Adult female, anal operculum, lateral; B, adult female, caudal rami showing ornamentation of pits in integument; C, Nauplius II, ventral; D, Adult female, anal operculum, dorsal. Scale bars A = 20 μ m, B = 40 μ m, C = 60 μ m, D = 25 μ m.

exopod with spinular row on distal margin anteriorly. Spine and seta formula as follows:

| | Coxa | Basis | Exopod | Endopod |
|-------|------|-------|-----------------|----------------|
| Leg 1 | 0-1 | 1-1 | I 1;I-1;III,1,4 | 0-1;0-1;1,1,4 |
| Leg 2 | 0-1 | 1-0 | I-1;I-1;III,1,5 | 0-1;0-2;1,1,4 |
| Leg 3 | 0-1 | 1-0 | I-1;I-1;III,1,5 | 0-1;0 2;1,1,4 |
| Leg 4 | 0-1 | 1-0 | I-1;I-1;II,1,5 | 0 1;0 2;1,II,2 |

Leg 5 (Fig. 18C) comprising single free segment, armed with 1 well developed outer spinulose seta, 1 strong inner spine ornamented with spinules, and 1 plumose seta in middle. Leg 6 (Fig. 18A) represented by 1 naked seta and 1 tiny spinule dorsolaterally.

Adult male

Body length: Mean \pm standard deviation = 732 \pm 47.45 μ m (range 673 to 769 μ m, n=10), mean body width 237 \pm 7.6 μ m



Fig. 20 *P. fimbriatus*. Adult female. A, Labrum, ventral; B, Mandible, posteroventral; C, Maxillule, ventral; D, Maxilla, posterior; E, Maxilliped, anterior. Scale bar in μm .

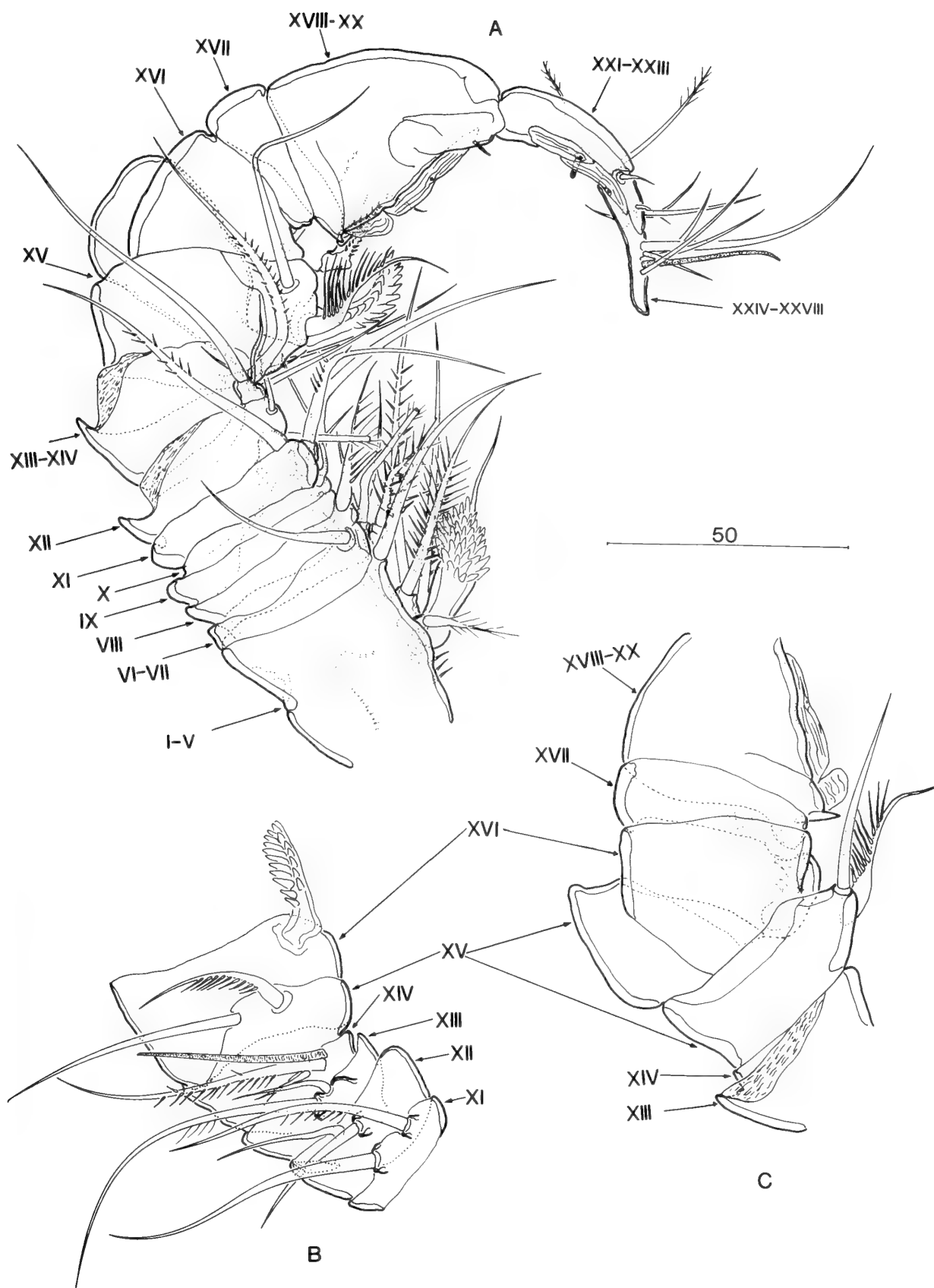


Fig. 21 *P. fimbriatus*. Male antennule. A, dorsal view. B, Detail of segments XI to XVI, anterior; C, Detail of segments XIII to XX, lateral view. Scale bar in μm.

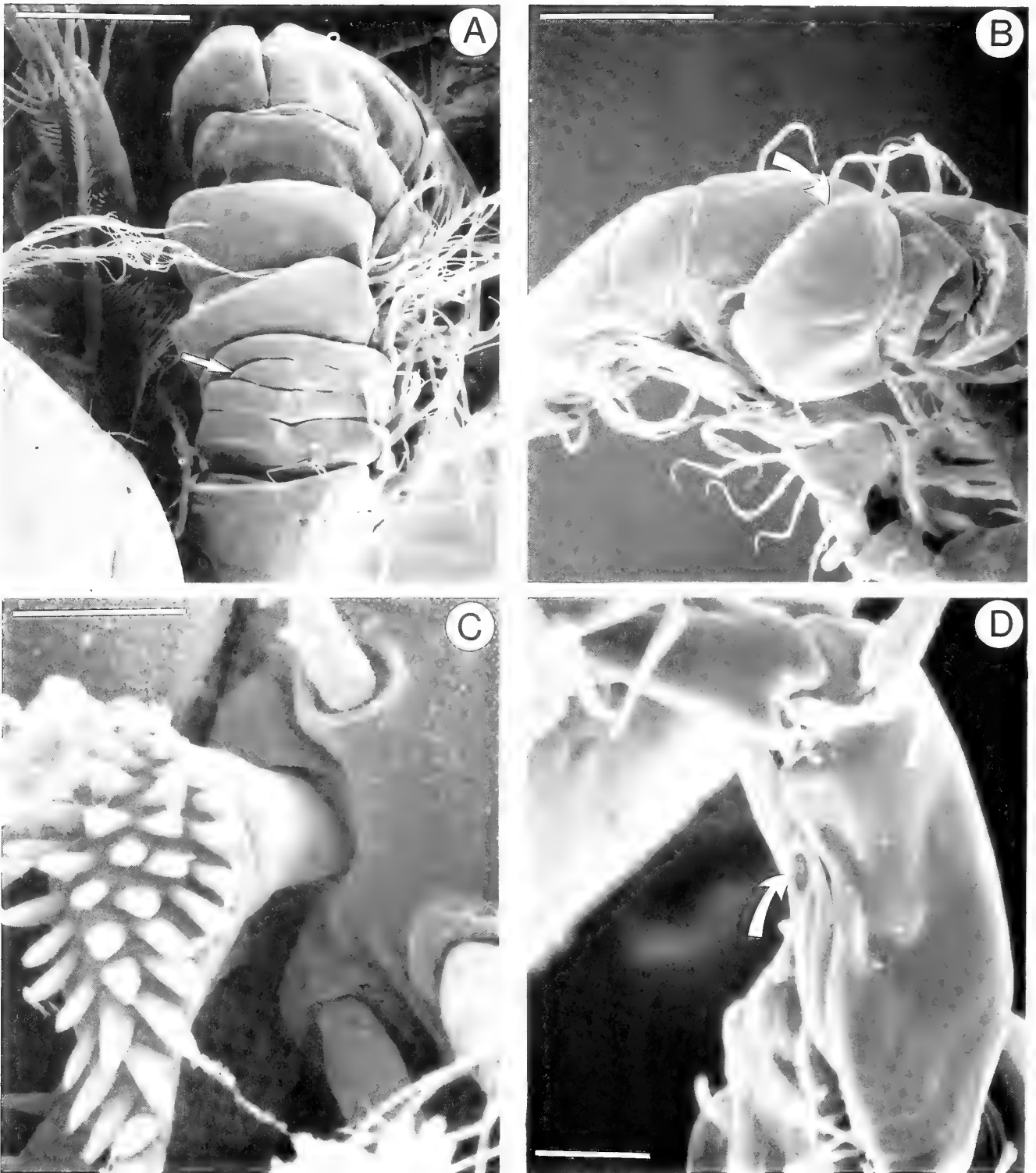


Fig. 22 Scanning electron micrographs of *P. fimbriatus*. Adult male antennule. A, Dorsal view, with segment 5 arrowed; B, Lateral view, with sheath on segment XV arrowed; C, Modified seta on proximal segment; D, Segment proximal to geniculation, with pore on modified element arrowed. Scale bars A = 30 μm , B = 25 μm , C = 6 μm , D = 5 μm .

(range 226 to 247 μm , $n=10$). Body (Fig. 17C) differing from adult female as follows: urosome 6-segmented, comprising fifth pedigerous, genital and 4 free abdominal somites; ornamentation of spinule rows as in Fig. 14D. Genital somite bearing paired genital apertures ventrally (Fig. 14C).

Caudal rami about 2.5 times longer than broad, ventral

surface unornamented. Large medial seta (V) relatively longer than in female.

Antennule 15-segmented (Figs 21A-C). Segment 1 armed with 9 setae; 1 seta large and modified (Fig. 22C), by ornamentation of strong spinules in proximal and mid sections, tapering to fine point distally; segment ornamented with curved

row of long spinules and row of minute spinules. Segment 2 with 4 setae. Segment 3 with 2 setae. Segments 4 and 5 partly fused, with segment 5 (arrowed in Fig. 22A) defined only on dorsal side, not ventrally. Segment 4 with 2 setae; segment 5 with 2 setae. Segment 6 with 2 setae. Segments 7, 8 and 9 separated from each other by extensive arthrodial membrane: segment 7 with 2 setae, segment 8 with 2 setae, and segment 9 with 2 setae plus aesthetasc. Segment 10 (= ancestral segment XV) produced on one side into extensive sheath (arrowed in Fig. 22B) enclosing segment 11 ventrally: armed with 2 setae, 1 ornamented with long spinules unilaterally. Segment 11 bearing curved seta ornamented with double row of strong denticles, plus 1 naked seta. Segment 12 partly fused to segment 13; armed with short seta ornamented with 2 rows of fine spinules, plus short naked seta. Segment 13 partly subdivided by partial suture: armed with short spinulate seta proximally, 2 short naked setae, plus 1 modified element attached to segment by short stalk, main part of element lying along surface of segment and ornamented with longitudinal ridges and small central pore (arrowed in Fig. 22D). Geniculation located between segments 13 and 14. Segments 14 and 15 partly fused, forming curved subchela-like section: segment 14 armed with 1 seta, 1 aesthetasc and 2 modified elements each ornamented with longitudinal ridges and a central pore, as distal element on segment 13. Apical segment tapering distally; armed with 11 setae and 1 aesthetasc, mostly originating on outer (= posterior) surface.

All other appendages as in female except for fifth (Fig. 14E) and sixth legs (Fig. 14F). Outer spinulose seta of leg 5 ornamented with some long setules distally. Sixth legs forming opercular plates bearing row of large spinules along ventral surface; armed with 1 inner spine, 1 well developed spinulose seta and 1 inner naked seta.

DISCUSSION

The number of naupliar instars in the Cyclopoida has been the subject of some controversy but it is clear, as Elgmork & Langeland (1970) strongly indicated, that there are normally 6 naupliar instars. This is supported by recent works on free-living freshwater Cyclopoida by Dahms & Fernando (1992, 1993, 1994) and by our data. The most difficult distinction is between nauplius IV and V and these stages have often been confused.

The complete naupliar sequence of *P. fimbriatus* was previously described by Ewers (1930) and Dukina (1956). Nauplius I and II were also described by Gurney (1933) but none of these provides setation counts of sufficient accuracy. Ewers (1930) described 6 stages but our descriptions differ as follows: antennule is 3-segmented not 4-segmented; antennary exopod is 4-segmented at N I and becomes 6-segmented, rather than remaining 4-segmented; caudal rami of N IV are represented by 2 pairs of setae and 1 pair of minute seta, rather than just 2 pairs of setae; ventral body surface is ornamented with spinular rows throughout the nauplius phase. In general, however, Ewers' drawings are so small that it is not worthwhile making detailed comparisons of appendage setation patterns.

Six naupliar stages were also described by Dukina (1956). Our descriptions differ from Dukina's as follows: antennule is 3-segmented; antennary exopod is 4-segmented at N I (given as 5-segmented by Dukina). Dukina's descriptions of appendage setation also lack sufficient detail for meaningful comparisons.

Gurney (1933) described the first 2 naupliar stages, but our

findings indicate that the caudal rami of N II are represented by a pair of setae not by 2 pairs as illustrated by Gurney. Apart from this discrepancy our results differ only in that the exopod of antenna is described as 3-segmented rather than 4-segmented as in our material.

The copepodid stages of *P. fimbriatus* were also partly described by Gurney (1933). Although our results are in substantial agreement, for example, with antennular segmentation throughout the copepodid phase, Gurney's drawings are not sufficiently accurate to permit comparisons of segmental setation.

Analysis of the antennular setation patterns of adult male *Paracyclops* permits the identification of the pattern of segmental homologies. The basic armature of each antennular segment in copepods is 2 setae plus one aesthetasc (Giesbrecht, 1892), with a few exceptions as identified by Huys & Boxshall (1991). Using this basic pattern, the 9 setae on the first segment of male *P. fimbriatus* indicate that it can be identified as representing 5 ancestral segments (segments I–V). The second segment, with 4 setae, can similarly be identified as derived from 2 ancestral segments (VI–VII). The third to twelfth segments all represent single ancestral segments (VIII to XVII), as indicated by the presence of a maximum of 2 setae on each. The fourth and fifth are incompletely separated (Fig. 22A) but we have treated them as distinct. The thirteenth segment has only 4 setae but is here identified as representing 3 ancestral segments (XVIII–XX). This decision is based on the presence of the neocopepodan geniculation between the thirteenth and fourteenth segments which unequivocally identifies the segmental boundary involved as XX to XXI, and on comparison with other cyclopids such as *Euryte robusta* Giesbrecht, 1900. In *E. robusta* males segment XVIII is separate and carries a long naked seta and a short spinulose seta, segment XIX–XX carries a short spinulose seta and a modified spine proximally and a slender seta distally (Huys & Boxshall, 1991). In *P. fimbriatus* the proximal part of the triple segment is defined by a partial suture marking the original plane between segments XVIII and XIX–XX. This part carries only a single spinulose seta and lacks the long seta; the distal part representing XIX–XX carries the same setation as in *E. robusta*. This confirms our interpretation of the thirteenth segment as a triple segment (XVIII–XX). The fourteenth and fifteenth segments, lying distal to the geniculation represent ancestral segments XXI–XXIII and XXIV–XXVIII, exactly as Huys & Boxshall (1991) found for *E. robusta*.

Compound antennular segments, such as the first and second segments of *P. fimbriatus*, were simply referred to as 'fused' by Huys and Boxshall (1991) in their comparative analysis of antennular segmentation patterns in all copepod orders, although such compound segments could be the result of two different developmental processes:

- 1) secondary fusion of segments that were separated earlier during ontogeny
- 2) failure of separation during development.

The compound first and second segments of the male antennule of *P. fimbriatus* result from the second process, the failure to separate. In contrast, the compound apical segment results from the secondary fusion of the sixth, seventh and eighth segments of the copepodid V stage. (The eighth segment of the copepodid V was already a compound segment, representing three ancestral segments XXVI–XXVIII which are not separately expressed by any known member of the order Cyclopoida).

Vertical tracking of the segmental boundaries as identified by their setation elements allows us to identify the homologies of

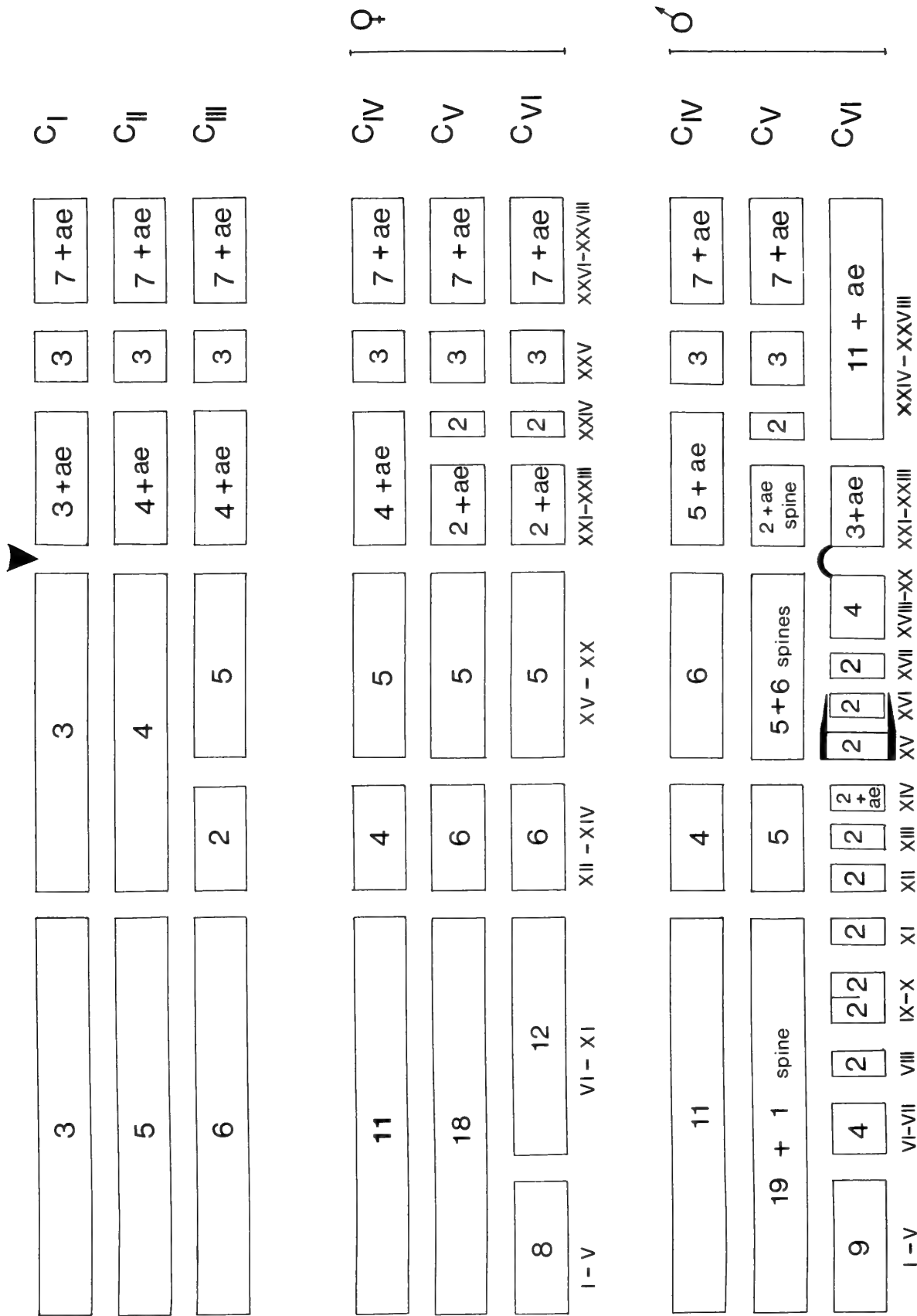


Fig. 23 *P. fimbriatus*. Schematic comparison of antennular segmental homologies in all copepodid stages of both sexes; showing location of geniculation and sheath in adult male as well as numbers of setae, spines and aesthetascs (ae) in all stages. [Roman numerals indicate derivations from hypothetical 28-segmented ancestral antennule proposed by Huys & Boxshall (1991); C_{VI} = adult.]

the segments of the female antennule and of the antennules throughout the copepodid phase of development. These results are presented in schematic form in Figure 23 which visually indicates homologous segmental boundaries expressed in successive copepodid stages. The aesthetasc derived from ancestral segment XXI provides a reference point throughout the copepodid phase: from the third segment of the first copepodid, to the fifth segment of the adult female and the fourteenth segment of the adult male. This, in concert with other setation features, confirms the unequivocal identification of the XX to XXI articulation (marked by the large arrow) in all stages. Identification of the homology of the more proximal segments relies on the presence of 11 setation elements on the third segment of the male copepodid V stage. These 11 elements testify to the segment's derivation from 6 unseparated ancestral segments (XV–XX) and indicates that the boundary between the second and third segments represents the XIV to XV articulation. Similarly, the presence of 5 setae on the second segment indicates that the boundary between first and second segments represents the XI to XII articulation. The remaining segmental homologies in all stages, including the adult female, can now be identified by tracking vertically through the male stages back to copepodids I and II and then forwards again to the adult female.

The seventh segment of the female antennule is identified as homologous with a single ancestral segment (XXV). The presence of 3 setae on this segment therefore requires explanation since the basic armature of segment XXV is 1 posterior margin seta plus 1 seta and 1 aesthetasc on the anterior margin (Huys & Boxshall, 1991). We suggest that one of the anterior elements may be a setiform aesthetasc and this should be investigated ultrastructurally.

This is the first time that the homologies of all antennular segments have been identified in all copepodid stages of both sexes of any cyclopoid copepod, with reference to the hypothetical 28-segmented antennule of the ancestral copepod (Huys & Boxshall, 1991). Within the family Cyclopidae antennular segmental numbers are frequently reduced and, indeed, many genera are characterised by their low segment numbers. The possible involvement of heterochrony in the reduction of antennular segmental numbers has already been noted. Gurney (1933) suggested that 'the reduced numbers of antennular segments in some species may be accounted for as the persistence of a larval character in the adult', pointing out that during development the last copepodid (Co V) typically has an 11-segmented antennule and that this number is commonly found in adults, as for example in *Microcyclops*.

Several authors working on cyclopids were aware of the importance of determining homologies between the different generic segmentation patterns and made detailed comparisons. Gurney (1933) reviewed earlier work by Claus (1893), Manfredi (1923), Lucks (1929) and Gelmini (1928) on the sequence of segmental subdivision during development in *Cyclops* species. He presented a tabular system showing derivations of a 17-segmented antennule and confirmed this pattern using his own data on *C. strenuus*. The strict determination of ancestral homologies of antennular segments provides new insight into the rather confused world of cyclopoid systematics at the generic level.

The scheme of segmental development (Fig. 23) indicates that at the moult from copepodid II to copepodid III it is the second segment that subdivides. This contrasts with the scheme presented for *P. fimbriatus* by Gurney (1933) who showed the first segment subdividing at this moult. We base our interpretation on the positions and relative lengths of the setae

on these segments. In particular a relatively long seta is positioned at the anterodistal angle of the first segment in copepodid II and 2 similarly long setae are present at the same position in copepodid III. Since no other setae of this length are present we interpret this as evidence of the constancy of the boundary marked by this seta and therefore conclude that the second segment has subdivided.

The setation of the second endopodal segment of the antenna increases progressively through the copepodid stages of *P. fimbriatus* in a very regular manner. The first copepodid stage possesses 4 setae distributed around the inner-distal angle of the segment (Fig. 8A). The seta which is located on the angle is slightly stouter than the other 3 and is here identified as seta VIII, using the numbering scheme proposed for another member of the family Cyclopidae by Boxshall & Evstigneeva (1994). The more distal seta is then identified as seta IX and the 2 more proximally located setae on the inner margin, as setae VII and VI. These 4 setae are presumably homologous with the proximal group of 4 setae present on the margin of the unsegmented endopod of the sixth nauplius stage (Fig. 3F). At each successive moult through the copepodid phase one additional seta is added proximally on the inner margin of the segment (Figs 8A–F). Thus at copepodid II a fifth seta (seta V) is added, at copepodid III a sixth seta (seta IV), and so on, until the final moult to adult (= copepodid VI) at which the ninth and final seta (seta I) is added.

The progressive development of the setation suggests that reductions in numbers of setae on the second endopodal segment, which are common within the family Cyclopidae, may be interpreted as resulting from heterochronic events. *Cryptocyclops bicolor* (Sars, 1863), for example, is a cyclopoid with only 7 setae on the second endopodal segment. This number is typical of the copepodid IV stage in both *Paracyclops* and the presumed ancestral cyclopoid stock, and may be interpreted as evidence that a neotenic event within the *Cryptocyclops* lineage has interrupted the progressive addition of setae.

The ontogeny of copepodid stages and examination the patterns of leg formation offer some evidence for inferring copepod phylogenetic relationships (Ferrari, 1988). A common pattern of development for legs 1–4, exhibited by at least 20 genera, was recognized by Ferrari. The pattern of development for the swimming legs of *P. fimbriatus* is in accordance with this common pattern as follows:

| Legs | 1 | 2 | 3 | 4 |
|------|-------------------|------------------|------------------|------------------|
| N | 1 [^] B; | 1 [^] B | | |
| I | 1+1; | 1+1; | 1 [^] B | |
| II | 2+2; | 2+2; | 1+1; | 1 [^] B |
| III | 2+2; | 2+2; | 2+2; | 1+1; |
| IV | 2+2; | 2+2; | 2+2; | 2+2; |
| V | 3+3; | 3+3; | 3+3; | 3+3; |
| VI | 3+3; | 3+3; | 3+3; | 3+3; |

(Where N = nauplius; Roman numerals = copepodid stages; 1[^]B = primary leg bud; 1+1 = reorganized leg with 1-segmented exopod and endopod; 2+2 = leg with 2-segmented exopod and endopod; 3+3 = leg with 3-segmented exopod and endopod).

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